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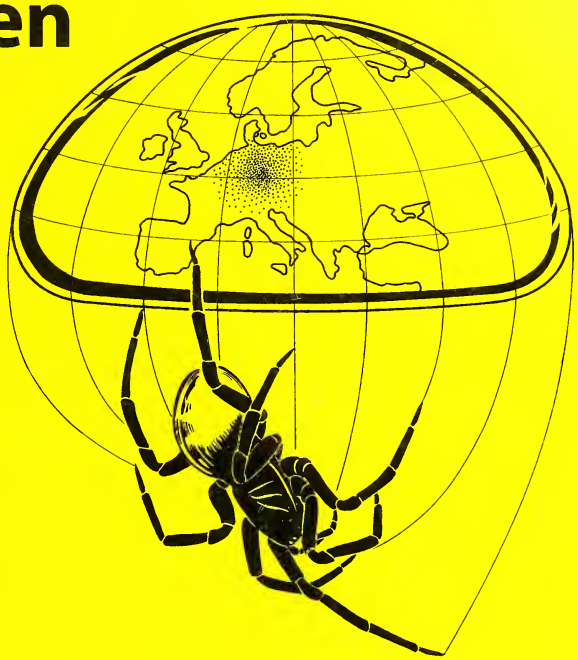

25TH ECA
EUROPEAN CONGRESS
OF ARACHNOLOGY

European Arachnology 2009

16.8. – 21.8.2009, Alexandroupoli, Greece
www.european-arachnology.org

Volume 40
ISSN 1018 -4171

Nuremberg, January 2011
www.AraGes.de/aramit

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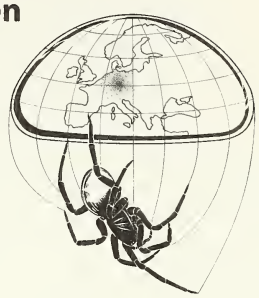

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Erscheinungsweise:
Pro Jahr 2 Hefte. Die Hefte sind laufend durchnummeriert und jeweils abgeschlossen paginiert.
Der Umfang je Heft beträgt ca. 50 Seiten. Erscheinungsort ist Nürnberg. Auflage von Heft 40: 750 Exemplare
Druck: Fa. Isensee, Oldenburg.

Autorenhinweise/Instructions for authors:
bei der Schriftleitung erhältlich, oder unter der URL: http://www.arages.de/aramit/

Bezug:
Im Mitgliedsbeitrag der Arachnologischen Gesellschaft enthalten (25 Euro, Studierende 15 Euro
pro Jahr), ansonsten beträgt der Preis für das Jahresabonnement 25 Euro. Die Kündigung der Mitgliedschaft oder des Abonnements wird jeweils zum Jahresende gültig und muss der AraGes bis 15. November vorliegen.

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IBAN DE75 4401 0046 0816 6274 66, BIC (SWIFT CODE) PBNKDEFF

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Preface

doi: 10.5431/aramit4001

The 25th European Congress of Arachnology was held in the city of Alexandroupolis, from 16 to 21 August 2009. It was jointly organised by the Department of Molecular Biology and Genetics of the Democritus University of Thrace and the Natural History Museum of the University of Crete. Arachnologists from all over the world arrived to this little point at the north-eastern border of Greece to attend this meeting, the 25th in a series which started in 1972 in Strasburg. The arachnological meeting has passed through many countries of Europe, but this was the first time that has taken place in Greece.

90 participants, including 30 students, from 28 representative countries from all five continents and 17 accompanying persons attended this meeting. The scientific programme comprised 51 oral presentations and 34 posters from various thematic fields such as taxonomy and faunistics, phylogenetics, biogeography, phylogeography, physiology, behaviour, ecology and others. 18 papers were submitted for evaluation for the proceedings volume and of these, 11 were selected for publication after peer review by two referees each. During the four days of scientific programme, three keynote presentations were given on special topics by: Miquel Arnedo, Victor Fet and Peter Jäger. Student awards were given to the best three oral presentations and the best three posters on the closing ceremony. Lectures: Holger Frick (Switzerland), Samuel Yu-Lung Hsieh (Germany), and Odile Bruggisser (Switzerland). Posters: Jin-Nan Huang (Taiwan), Vera Opatova (Czech Republic), and Chueh Hou (Taiwan).

During the five-day stay at the congress hall of the Alexander Beach Hotel, participants had the opportunity to enjoy the hospitality of the staff, but also to take advantage of the beautiful beach opposite the hotel and the cosy atmosphere of Greek taverns. Accompanying persons visited the most important archaeological sites, cities and natural reserves of the area. During the mid-week excursion, all of us had a wonderful experience canoeing on the Nestos river or walking by its riverbank and then enjoying the food, wine and nice view of a local tavern in the surroundings of the city of Xanthi, where we spent the rest of the day. An opening ceremony at the pool of the hotel, the standard 'Russian party', Thursday's congress dinner, and finally a beach party at the end of the congress completed the picture of a very pleasant week.

The General Assembly of the ESA members closed the meeting of 2009. During this ceremony we had to say our last goodbyes to the late arachnologists Gershom Levy and Jean-Pierre Maelfait who passed away that year. Nevertheless, we also had to congratulate the 70th anniversary of the still very active arachnologist Christo Deltshev. Members of the Society had to vote on the fate and form of the proceedings of the congress, which later in the year lead to a general referendum. Proceedings should thus retain their paper format and be distributed to all members of the Society, either edited by an existing journal or – eventually – by the Society's official future journal.

Scientific contributions and exchange of knowledge harmonised with relaxation and fun due to the commitment of many people who volunteered to offer their help: first of all Iasmi Stathi and Katerina Spyridopoulou did their best for the whole year's organisation procedure; our students Eleni Panayiotou, Aggeliki Paspati, Kyriakos Karakatsanis and Stavros Gogolopoulous, assisted in various ways during the congress week; Pavlos Georgiadis was the main group leader of the accompanying people's

activities and Emma Shaw assisted in the secretariat, as well as other activities; without Peter Jäger there would never have been such a successful last day beach party, since he was the night's DJ. Many participants also assisted with the smooth running of the week's programme, among them session chairs, members of the scientific committee and evaluation teams. I am deeply grateful to the staff of the Alexander Beach Hotel for their patience and kindness, all the facilities they provided and the very well organised service. I also owe my gratitude to Theo Blick and the rest of the Arachnologische Mitteilungen personnel for our excellent cooperation during editing of the proceedings and the numerous reviewers who volunteered to check and decide upon the selected papers of this volume.

I finally have to acknowledge our sponsors: the local authorities, Prefectural Self-Government Prefecture of Evros; Prefecture of Rhodopi-Evros; Region of Macedonia-Thrace; the Democritus University; the European Society of Arachnology. Special thanks to all secretary members of the above offices who offered their support and help at any moment as well as the members of the ESA council not only for financial support, but also for the psychological and consulting support during the whole year of the organisation of this congress.

Maria Chatzaki

When citing the whole volume, please use:

CHATZAKI M., T. BLICK & O.-D. FINCH (Eds) (2011): European Arachnology 2009. Proceedings of the 25th European Congress of Arachnology, Alexandroupoli, 16–21 August 2009. – Arachnologische Mitteilungen 40: 1-109

The contributions to this volume are online available at:
1. http://arages.de/aramit
2. http://www.european-arachnology.org/collo/collo25.shtml
3. http://www.mbg.duth.gr/en/index.php?cid=84&st=1

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Abundant and rare spiders on tree trunks in German forests (Arachnida, Araneae)

Theo Blick

doi: 10.5431/aramit4002

Abstract: The spider fauna active on the bark of trees in forests on eight sites in different regions in Germany was investigated. Trunk eclectors at about 2-4 meters height on living trees were used in different regions of Germany (SW Bavaria, Hesse, Brandenburg) between 1990 and 2003. In Hesse eclectors were also used on dead beech trees (standing and lying). In this study data, mainly from beech (*Fagus sylvatica*) and spruce (*Picea abies*), from May to October are compared – whole year samples (including winter) are only available from Hesse. A total of 334 spider species were recorded with these bark traps, i.e. about one third of the spider species known from Germany. On average, each of the eight regions yielded 140.5 (± 26.2) species, each single tree 40.5 (± 12.2) species and 502 (± 452) adult spiders per season (i.e. May to Oct.). The 20 most abundant species are listed and characterised in detail. Six of the 20 species were not known to be abundant on bark, three prefer conifers and three beech/broadleaf. Even in winter (December-March) there was a remarkably high activity on the trunks. However, only a few species occur exclusively or mainly in winter. Finally, the rarity of some bark spider species is discussed and details (all known records in Germany, phenology) of four of them are presented (*Clubiona leucaspis*, *Gongylidiellum edentatum*, *Kratochviliella bicapitata*, *Oreonetides quadridentatus*). The diversity and importance of the spider fauna on bark in Central Europe is still underestimated.

Key words: bark, common species, distribution, eclectors, Germany, rare species

The spider fauna of tree trunks in Germany and Central Europe is much less well known than the epigeal fauna active on the forest floor. Only the fauna of the tree crowns is more poorly known (SIMON 1995, GOSSNER 2004, RÖDER et al. 2010). Furthermore, the epigeal spider fauna of common forest types – at least in Central Europe – is significantly less intensively investigated than that of the epigeal fauna of special habitats, such as those that are extremely dry or wet (HÄNGGI et al. 1995). I estimate that this disproportion is much higher, if one compares the epigeal spider fauna in forests with the tree trunk spider fauna. In Central European forests knowledge about the tree trunk fauna reaches an estimated maximum level of 5% compared with the epigeal fauna.

Before the research in Strict Forest Reserves in Hesse started, estimates of the species richness of animals (biodiversity) in a beech forest were 1500-2000 species (all animals) (ELLENBERG et al. 1986). Now we know that there are closer to 5000-6000 (DOROW et al. 2004, 2010). In each of the four Strict Forest Reserves investigated until now 162 to 202 spider species were recorded (BLICK 2009).

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submitted: 13.1.2010, accepted: 15.4.2010; online: 10.1.2011

As the complete spider coenoses and species lists were already published (see below) or will be published elsewhere, the focus here is on the following topics: (a) totals of species and abundances, (b) the 20 most abundant spider species, (c) winter activity, and (d) notes on rarely or very rarely recorded species.

Methods

Trunk eclectors (Fig. 1, method after BEHRE 1989, see also BRAUN 1992, DOROW et al. 1992, ENGEL 1999) at heights from 2 to 4 meters on living trees were used in different regions of Germany (SW Bavaria, Hesse, Brandenburg) (Fig. 2). In Strict Forest Reserves in Hesse eclectors were also used on dead beech trees (on standing trees and with an adapted type of trap, also on lying trees) (DOROW et al. 1992).

The traps were operated during different time periods in the different regions and projects. The trapping periods from May to October were available for comparison from nearly all sites (except Brandenburg). Hesse (Strict Forest Reserves) was the only area where data were available for the whole year, i.e. two entire years including two winters.

Most data sets are from beech – *Fagus sylvatica* and spruce – *Picea abies*; see details below.

Figure 1: Trunk eclectors on standing beech trees in northern Hesse, Germany, a – spring, b – winter, c – dead tree

Sites

The data included in this study came from different sites in Germany (Fig. 2):

- Three pairs of pine forests, also part mixed with beech and oak, in Brandenburg (no. 1 in Fig. 2, two forests in the north, one in the south) (unpubl. data from 2000 and 2001, June to September, leg. T. Taeger & U. Schulz, det. TB). In each of the six forests six trunk eclectors were installed on Scots pine – *Pinus sylvestris*. A total of 36 trees were investigated.

- In four Strict Forest Reserves and their reference areas, where forestry is continued, in Hesse (nos. 2-5 in Fig. 2) trunk eclectors were installed on two living and two dead standing beech trees during two whole years (MALTEN 1999, 2001, MALTEN & BLICK 2007, BLICK 2009). Additionally at least two eclectors on lying dead beech trees were installed in each reserve. In total 30 standing and 13 lying dead trees were investigated.
- Mixed forest ('Stadtwald'), between the urban area of Frankfurt am Main and its airport. 12 trees (alder – *Alnus glutinosa*, ash – *Fraxinus excelsior*, birch – *Betula pendula*, two beeches, douglas fir – *Pseudotsuga menziesii*, elm – *Ulmus laevis*, Scots pine, two common oaks – *Quercus robur*, sessile oak – *Quercus petraea*) were investigated with trunk eclectors in 2000 (beginning of February/mid-March to beginning of November) (MALTEN et al. 2003, det. in part by TB) (no. 6 in Fig. 2).
- Forest near Biburg, east of Augsburg, Bavaria (no. 7 in Fig. 2); eight young beeches, four young spruces (20-40 y), two older beeches, two older spruces (about 100 y); beginning of April to end of October 1996 (ENGEL 1999, 2001, det. mainly by TB).
- Forests near Krumbach and Ottobeuren, Bavaria (no. 8 in Fig. 2); 16 beeches, eight douglas firs, eight common oaks, two northern red oaks – *Quercus rubra*, two silver firs – *Abies alba*, 22 spruces (unpubl. data from 1999 to 2003, April to October, with exceptions of 1999 (beginning in June) and of 2000 (until November), leg. K. Engel & M. Gossner, det. TB).

Table 1: Totals of the spiders in the trunk eclectors from the 8 sites

region no.	species	adults
1	123	6174
2	116	7796
3	130	10375
4	149	8399
5	149	6685
6	174	9283
7	106	4904
8	177	44712

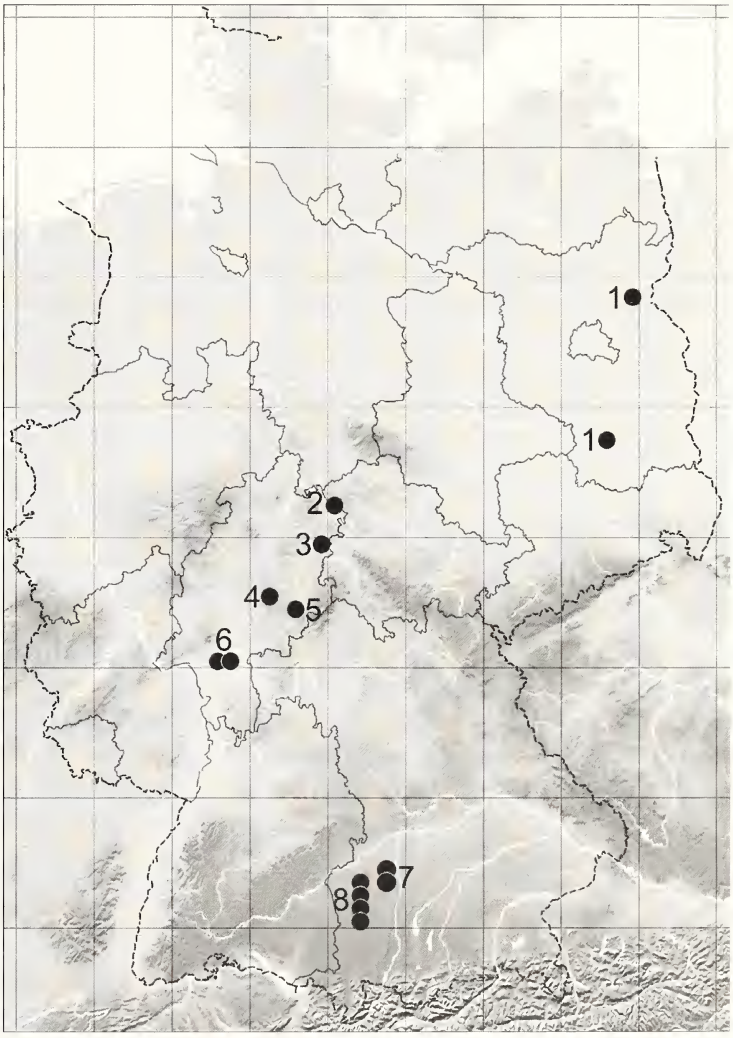

Figure 2: Sites with trunk eclectors in Germany, included into this study 1: forests in Brandenburg (Blick & Schultz unpubl.); 2-5: Strict Forest Reserves in Hesse (2: Hohestein, MALTEN & BLICK 2007; 3: Goldbachs- und Ziebachsrück, BLICK 2009; 4: Niddahänge östlich Rudingshain, MALTEN 1999; 5: Schönbuche, MALTEN 2001); 6: Stadtwald, Frankfurt am Main, Hesse (MALTEN et al. 2003); 7: forest near Biburg, east of Augsburg, Bavaria (ENGEL 1999, 2001); 8: forests near Krumbach and Ottobeuren, Bavaria (Blick et al. unpubl.); see text.

Results

Totals

In total 334 spider species, i.e. one third of the spider fauna of Germany, were recorded with 98328 adult spiders. In the 8 different regions between 106 and 177 spider species were recorded, with an average of 140.5 species (± 26.2 standard deviation) (Tab. 1).

Between 21 and 88 spider species were recorded per tree and season (i.e. May-Oct. – based on 115 living trees/season and a total of 298 species), with an average (Ø) of 40.5 species (± 12.2). Altogether 122 to 2696 adult spiders per tree and season were trapped, Ø 502 (± 452).

Twenty most abundant spider species

In Tab. 2 the 20 most abundant spider species are sorted in descending abundance. Regional distribution (focus or exclusivity – if nothing is noted the species was recorded in every one of the 8 regions), the tendency to occur on broadleaves/conifers and other notes are added.

To summarise:

- 8 of the 20 species (40%) were linyphiids, 10 families were present
- only 2 species belong to the same genus (*Xysticus*)
- 6 species are not known yet as abundant bark species (compare e.g. WUNDERLICH 1982)
- 14 species are abundant in (nearly) all regions investigated, 6 species have a more regional distribution
- 3 species prefer conifers, 3 species prefer beeches/broadleaves [3 other species were only or mainly trapped in regions, where all/most of the traps were on beech/broadleaf]
- these 20 most abundant species make up 65281 adults, i.e. 66.4 % of the adult spiders from the trunks

Most abundant spider species active in winter

A similar analysis was made for the winter active species (trapping months December to March, including long winter trapping periods in the regions which ended at the end of April or even at the beginning of May in some years). This means that mainly data of the regions 2-5 (see Fig. 2) and only some additional data of region 6 could be analysed. All these data came from the federal state Hesse. A total of 140 species, 7356 adults and 15714 juveniles (9833 determinable to species level) were recorded during the winter periods.

Even in winter, numerous spiders were found in the trunk eclectors. Only two representatives of the commonly known winter-active spiders (e.g. the linyphiid genera *Centromerus*, *Macrargus* and *Walckenaeria*; the dictynid *Cicurina*) are on this list (Tab. 3). The majority of the species are also included in Tab. 2. Compared to the forest floor, fewer species on bark were exclusively active in winter. Only *Cicurina cicur* and *Thyreosthenius parasiticus* can strictly be placed in the latter category, but at some sites also *Monocephalus castaneipes*. The 9 species with more than 100 adult individuals comprise 5930 (81%) of the adult spiders from the trunks in the winter – a much less balanced pattern than in the summer (see above).

Rare spider species

There are several 'types' of rare spider species: (a) widely distributed but rare, (b) at or near the border of their distribution area, (c) with restricted distribution areas (Central European endemics?). Examples of species for these types are listed as follows: species name (family), adults recorded (ind.), and distribution area. PLATNICK (2009), STAUDT (2009) and MIKHAILOV (1997) were used as main sources for the total distribution of each species.

(a) widely distributed but rare

Araneus saevus (L. Koch, 1872) (Araneidae), 2 ind., Holarctic

Carrhotus xanthogramma (Latreille, 1819) (Salticidae), 59 ind., Palaearctic

Dendryphantes hastatus (Clerck, 1757) (Salticidae), 32 ind., Palaearctic

Dipoena torva (Thorell, 1875) (Theridiidae), 120 ind., Europe to W Siberia

Mastigusa arietina (Thorell, 1871) (Dictynidae), 3 ind., Europe

Philodromus buchari Kubcová, 2004 (= *P. longipalpis* auct. in Central Europe) (Philodromidae), 19 ind., Europe and Turkey

Stroemiellus stroemi (Thorell, 1870) (Araneidae), 1 ind., Palaearctic

Interestingly there are no records of the very rare tree-living species *Philodromus poecilus* (Thorell, 1872) (Philodromidae), Palaearctic (see MUSTER 2009) and *Xysticus albomaculatus* Kulczyński, 1891 (Thomisidae), Germany to Romania, probably Russia (see JANTSCHER 2001).

(b) at or near the border of their distribution

Cinetata gradata (Simon, 1881) (Linyphiidae), 76 ind., central and southern Europe, mainly in mountainous areas, its northern border of distribution is situated in Germany.

Clubiona leucaspis Simon, 1932 (Clubionidae) (Figs. 3a, 4a), 583 ind., southern and central Europe, i.e. the northern border is located in Germany, in Germany only in the north-eastern and south-western

Table 2: The twenty most abundant bark spider species (see text)

species (family) (**bold** = not well known as bark species)	adults recorded	regional focus or exclusivity (nos. see fig. 2)	tendency to/focus on tree types	notes
Hahnia pusilla C.L. Koch, 1841 (Hahniidae)	15308	7 & 8, single specimens in 3 & 5		only 58 males, females also on the forest floor, males mainly on the floor
Amaurobius fenestralis (Ström, 1768) (Amaurobiidae)	8780			also juveniles were determined (in total 16579), also on the forest floor
Pelecopsis elongata (Wider, 1834) (Linyphiidae)	5186	7 & 8		rarely also found on the forest floor or in scree and talus habitats
Drapetisca socialis (Sundevall, 1833) (Linyphiidae)	5087		slight preference for beech	also 3145 juv. recorded
Xysticus audax (Schrank, 1803) (Thomisidae)	4106		preference for conifers	
Walckenaeria cuspidata Blackwall, 1833 (Linyphiidae)	3076	2 & 3, few in 4	[2-4: only traps on beech]	also on the forest floor
Enoplognatha ovata (Clerck, 1757) (Theridiidae)	2691			
Lathys humilis (Blackwall, 1855) (Dictynidae)	2630	mainly 8, not 3	slight preference for conifers	
Moebelia penicillata (Westring, 1851) (Linyphiidae)	2300			
Neon reticulatus (Blackwall, 1853) (Salticidae)	1897	majority in 8	slight preference for conifers	only 17 males, both sexes mainly on the forest floor
Cryphoeca silvicola (C.L. Koch, 1834) (Hahniidae)	1837	mainly 8, not 1 & 6		also on the forest floor
Entelecara erythropus (Westring, 1851) (Linyphiidae)	1574	2-6 (Hesse)	[2-6: most traps on beeches/broadleaf]	also on the forest floor
Coelotes terrestris (Wider, 1834) (Amaurobiidae)	1525	not 1	preference for beech	mainly on the forest floor
Xysticus lanio (Schrank, 1803) (Thomisidae)	1504		preference for broadleaf	
Lepthyphantes minutus (Blackwall, 1833) (Linyphiidae)	1491			
Philodromus collinus C.L. Koch, 1835 (Philodromidae)	1381			rarer on the forest floor
Meioneta innotabilis (O. P.-Cambridge, 1863) (Linyphiidae)	1358	not 3, rare in 2 ,4, 5, 7		
Diplocephalus cristatus (Blackwall, 1833) (Linyphiidae)	1288	2 & 3, singleton in 4	[2-4: only traps on beech]	mainly on the forest floor, also in open land habitats
Harpactea hombergi (Scopoli, 1763) (Dysderidae)	1170	mainly 6, few in 3 & 8		also on rocks and walls
Anyphaena accentuata (Walckenaer, 1802) (Anyphaenidae)	1092	not 4		also juveniles can be determined (in total 10322), rare on the forest floor

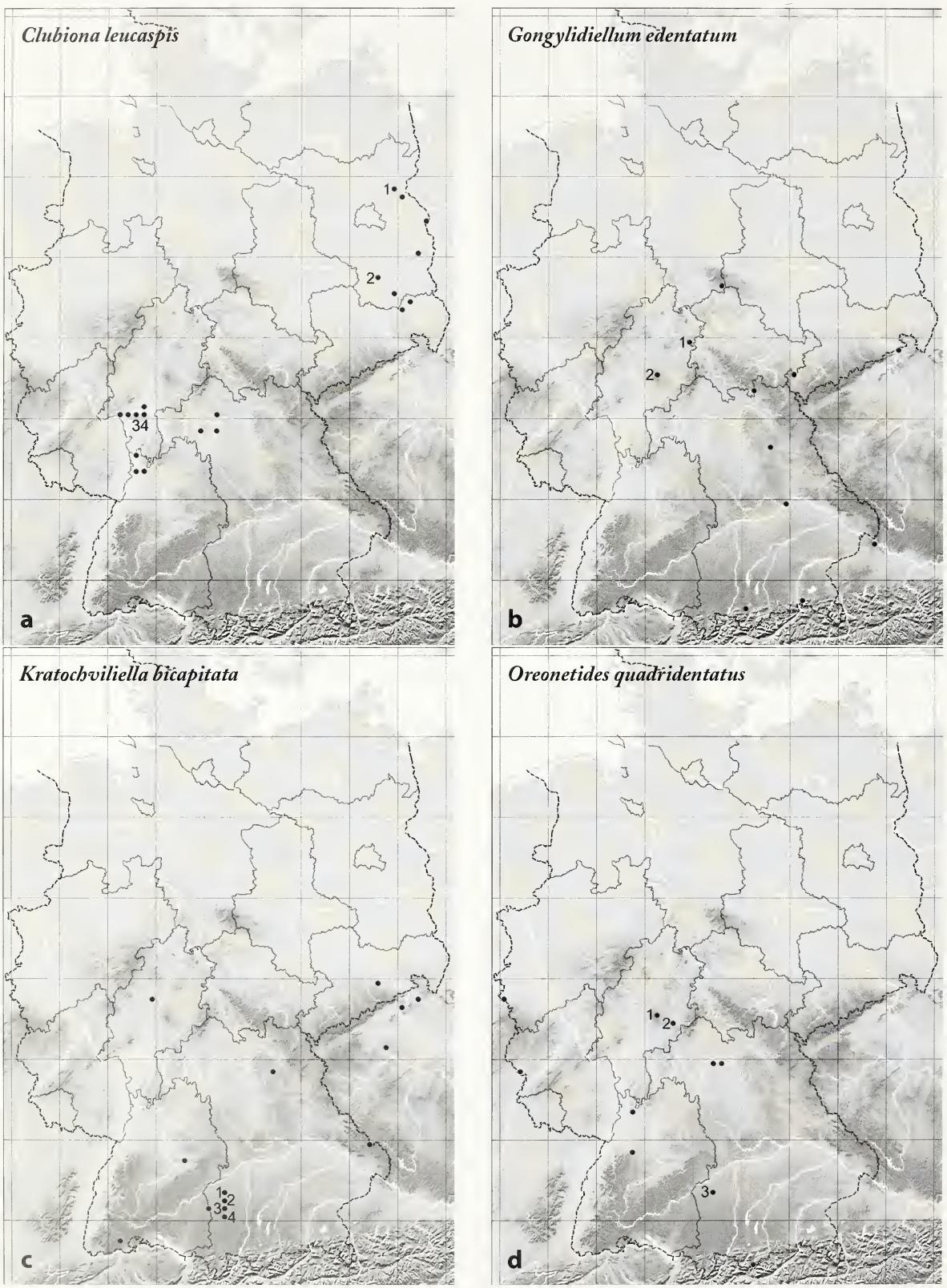

Figure 3: Distribution maps for Germany of four of the rare spider species (after STAUDT 2009); a *Clubiona leucaspis*, 1 & 2: Blick & Schultz (unpubl.); 3 & 4: MALTEN et al. (2003); b *Gongylidiellum edentatum*, 1: BLICK (2009), 2: MALTEN (1999); c *Kratochviliella bicapitata*, 1-4: Blick et al. (unpubl.); d *Oreonetides quadridentatus*, 1: MALTEN (1999), 2: MALTEN (2001), 3: Blick et al. (unpubl.)

Table 3: Most abundant winter active spider species (>100 specimens)

species (family – only when the species is not present in Tab. 2)	ad./juv.	regional focus or exclusivity (nos. see fig. 2)	winter activity (if > 50 %)	notes (additional to Tab. 2)
adults				
Amaurobius fenestralis (Ström, 1768)	2391			87 % males
Walckenaeria cuspidata Blackwall, 1833	1685	2 & 3, few in 4	55 %	
Monocephalus castaneipes (Simon, 1884) (Linyphiidae)	839	only 4 & 5	81 %	also on the forest floor
Cicurina cicur (Fabricius, 1793) (Dictynidae)	292	not 6	77 %	also on the forest floor
Moebelia penicillata (Westring, 1851)	156			
Thyreosthenius parasiticus (Westring, 1851) (Linyphiidae)	156	not 5	74 %	rarely on the forest floor
Diplocephalus cristatus (Blackwall, 1833)	147	only 2 & 3		
Drapetisca socialis (Sundevall, 1833)	140			
Labulla thoracica (Wider, 1834) (Linyphiidae)	124	not 6		also on the forest floor
juveniles				
Anyphaena accentuata (Walckenaer, 1802)	4555	not 4	59 %	
Amaurobius fenestralis (Ström, 1768)	3105			
Diaea dorsata (Fabricius, 1777) (Thomisidae)	905			
Clubiona leucaspis Simon, 1932 (Clubionidae)	557	only 6		see section 'rare spider species'
Cryphoeca silvicola (C.L. Koch, 1834)	199	not 6	75 %	
Lathys humilis (Blackwall, 1855)	111	not 2 & 4	84 %	

regions with the highest average temperatures, only lowlands. First record for Germany by MALTEN (1994). Note: some records of *C. genevensis* L. Koch, 1866 on trees might really represent further records of *C. leucaspis*. For the typical colouration see: http://spiderling.de/arages/Fotogalerie/species_fg.php?name=Clubiona%20leucaspis (STAUDT 2009).

Clubiona marmorata L. Koch, 1866 (Clubionidae), 64 ind., central to south-eastern Europe, its north-western border is situated in Germany.

Monocephalus castaneipes (Simon, 1884) (Linyphiidae), 1035 ind., central to northern, western and south-western Europe, eastern border in Germany.

Theridion boesenbergi Strand, 1904 (Theridiidae), 105 ind., central and eastern Europe, without northern parts, mainly in mountainous areas, northern border in Germany.

(c) with restricted distributions; central European 'endemics' (all belong to the Linyphiidae)

Gongylidiellum edentatum Miller, 1951 (Figs. 3b, 4b, 10 ind., central Europe (Germany, Czech Rep., Austria), N Italy, SE France, most numerous record (31 specimens) is from a rotting beech stump in Hesse (BLICK 2009), see also below.

Kratochviliella bicapitata Miller, 1938, 878 ind., central Europe (Germany, Austria, Czech Rep., Slovakia, Poland), Bulgaria; besides the specimens presented here there is just one other record of a larger number of individuals in Poland (CZAJKA & BEDNARZ 1972: "only on the northern surface of the tree trunks. ... We estimated that the whole population consisted of some 6000-7000 specimens at that time"), see also below.

Oreonetides quadridentatus (Wunderlich, 1972), 82 ind., central Europe (Germany, Austria, Luxembourg) and one record with four specimens from the French Pyrenees (BOSMANS et al. 1986); the

record presented here probably refers to the greatest number of individuals found until now.

Pseudocarorita thaleri (Saaristo, 1971), 64 ind., central Europe (Germany, Czech Rep., Austria, Switzerland, Belgium).

More details on four of the rare species mentioned above are presented in Figs. 3 and 4, because very little information has previously been published on them. The phenologies of these four species are presented in Fig. 4. The trapping periods are assigned to the month to which the majority of the days of each trapping period belonged; this may not be the month in which the trap was changed or emptied. For *Gongylidiellum edentatum* and *Kratochviliella bicapitata* supplementary data are included, i.e. unpublished data from other sites, or from the sites mentioned in this paper but caught with methods other than trunk eclectors.

Discussion

TOFT (1976) caught 3195 spiders from the end of April to mid-December with 'arboreal photoeclectors' (method after NIELSEN 1974) but gave no species number for the individual methods used (total species number = 147). ALBERT (1982) was the first to publish detailed data from trunk eclectors (method after FUNKE 1971, i.e. without trapping bottles at the bottom; by contrast the type after BEHRE 1989 uses bottles at the bottom, Fig. 1). The eclectors were installed on beeches and spruces and were operated from March/April to November/December in 1969 and 1971. He gives no total species number for the trunk eclectors, but for the four investigated types: spruce old (52 species, 4025 adults), spruce young (39 sp., 972 ad.), beech old (67 sp., 1525 ad.), beech young (33 sp., 199 ad.). PLATEN (1985, also with the eclector type of FUNKE 1971) recorded 74 species over two whole years, 69 on beech and 37 on spruce.

Some other examples: BRAUN (1992), who already used the eclector type of BEHRE 1989, caught 108 spider species (3709 adults) on trunks of Scots pine at 3 different heights above the forest floor (1, 4 and 8 meters) from May to Oct. SIMON (1995), also trapped on Scots pine and at different heights (1.5, 5, 10 and 13 meters – species numbers 71, 59, 48, 35, i.e. lower numbers at increasing height), over 3 whole years collecting a total of 103 species (including traps on branches in the crown). GOERTZ (1998) examined 10 trees (5 crack willows – *Salix fragilis*, 2 almond willows – *Salix triandra*, 3 black poplars – *Populus* aff. *nigra*) from mid-December to end of June and caught a total of 100 species and 20167 determinable

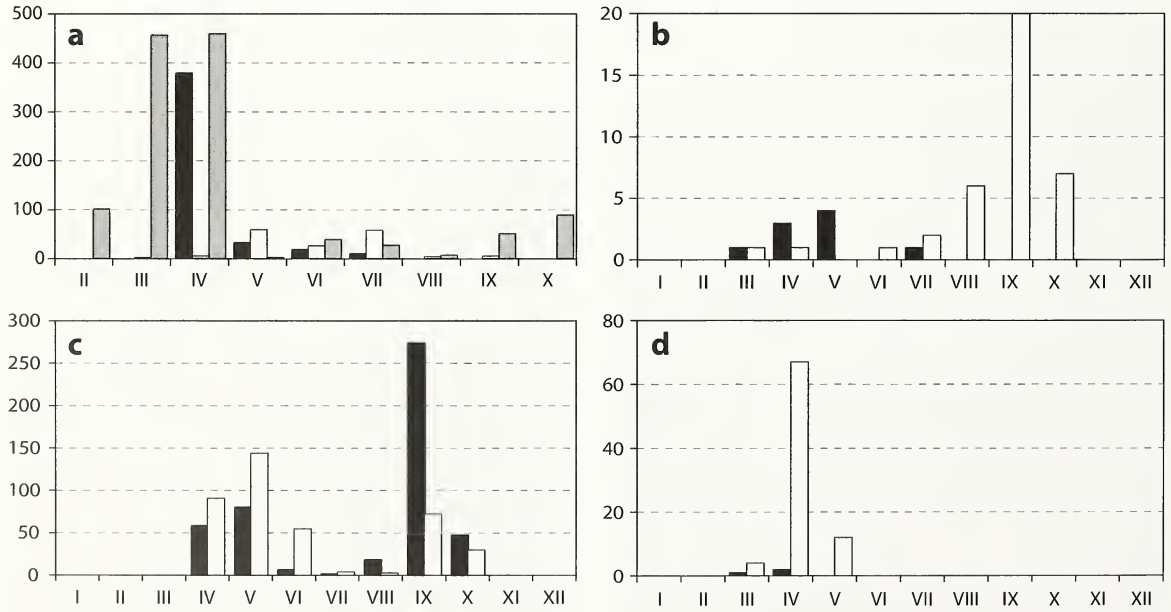

Figure 4: Phenology of (a) *Clubiona leucaspis*, (b) *Gongylidiellum edentatum*, (c) *Kratochviliella bicapitata*, (d) *Oreonetides quadridentatus* (black males, white females, grey juveniles; x-axis: Roman numerals represent the months; y-axis: numbers of trapped specimens); a *Clubiona leucaspis* (no traps operated from November/XI to January/I), totals 441♂♂, 159♀♀, 1231 juv.; b *Gongylidiellum edentatum*, totals 12♂♂, 45♀♀ (incl. 3♂♂, 7♀♀ in long winter periods, i.e. Nov./Dec. to end of April/beginning of May – not included in this graph); c *Kratochviliella bicapitata*, totals 490♂♂, 399♀♀; d *Oreonetides quadridentatus*, totals 4♂♂, 83♀♀ (incl. 1♂ in a longer winter period, i.e. mid Nov. to mid of March – not included in this graph)

specimens. Details: 29-55 species (Ø 41.2 ± 8.8), 580-3422 spiders (Ø 2017 ± 918). FINCH (2001) caught from spring to autumn on 6 living trees (3 beeches, 2 oaks, 1 Scots pine – open type after FUNKE 1971) 110 species (Ø 35.2 ± 15.3), and 56 species on two lying dead trees.

All these data fit in the ranges given above for single trees. The eclector type without a bottle traps fewer specimens (and presumably less species) than the type with a bottle. Nevertheless, data from the bottle-less type fit within the range. A possible reason: the range of species and specimen numbers on older trees (with a larger diameter) compared to younger trees is larger than the range resulting from trap type. The data from different regions in this paper already show that it is difficult to compare the published data. The reasons are that different trapping periods, different tree ages and diameters and finally different types of eclectors were used. Nevertheless, important conclusions can be drawn (see also BLICK 2010):

- spiders are a species rich group on forests floors, as well as on trees;
- to estimate their biodiversity in forests data from both the forest floor and from trees are necessary;
- the majority of the dominant species do not prefer conifers or broad-leafed tress; instead they are widely distributed;
- in Germany forest spider species that are restricted in their distribution to Central Europe (s.l.) occur;
- the diversity and importance of the spider fauna on bark in Central Europe was until now underestimated compared with the epigeal fauna (even though there is an overlap of both coenoses).

Acknowledgements

My thanks go: to Andreas Malten (Frankfurt am Main), who determined the spiders of three strict forest reserves and to Ingmar Weiss (Grafenau-Rosenau), who determined a part of the spiders from Frankfurt; to the whole team of the Strict Forest Reserve Project, especially to Wolfgang Dorow (Frankfurt am Main), the old stager of the project; to Aloysius Staudt (Schmelz) for his great work on the German www-distribution maps; to Tim Taeger and Ulrich Schultz (Eberswalde) for their field and lab work; to Kerstin Engel, Martin Goßner (formerly Freising), and Andreas Malten for collecting the spiders and for arranging finances; last but not least to Andrew Liston (Müncheberg) for improving the English. Research on the Strict Forest Reserves in Hesse was conducted in cooperation with and financially supported by the 'Landesbetrieb Hessen-Forst'.

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On some new or rare spider species from Lesbos, Greece (Araneae: Agelenidae, Amaurobiidae, Corinnidae, Gnaphosidae, Liocranidae)

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doi: 10.5431/aramit4003

Abstract: In this paper, three new spider species are described from the Greek Aegean island Lesbos: *Tegenaria maelfaiti* sp. nov. (Agelenidae), *Amaurobius lesbius* sp. nov. (Amaurobiidae) and *Agroeca parva* sp. nov. (Liocranidae), as well as the unknown male of *Arabelia pheidoleicomes* Bosselaers, 2009 (Corinnidae). Diagnostic features and notes on ecology and distribution of these species are given. Two new records for the island are provided, such that currently 300 spider species are known from Lesbos.

Key words: *Agroeca*, *Amaurobius*, *Arabelia*, description, new species, *Tegenaria*

The spider fauna of Greece is still poorly known compared to other Mediterranean countries. Recently, BOSMANS & CHATZAKI (2005) reported 856 species known from Greece. In a study of one relatively small region, the Nestos delta, BUCHHOLZ (2007) added 61 spider species to the Greek fauna. The spiders of the island Lesbos were recently surveyed by a group of Belgian arachnologists during several collecting trips (October 2007, March-April 2008, May-June 2008). This resulted in a catalogue of 292 species, some of them new to science. Among these, VAN KEER & BOSMANS (2009) described four new dysderid species. The current paper provides the description of three more new species, belonging to the families Agelenidae, Amaurobiidae and Liocranidae and the description of the unknown male of another liocranid genus.

Material and Methods

The material treated in this paper was collected by members of the Belgian Arachnological Society ARABEL during several trips to Lesbos, as detailed in BOSMANS et al. (2009).

Specimens were examined and illustrated using a Wild M5 stereomicroscope. Further details were studied using an Olympus CH-2 stereoscopic microscope with a drawing tube.

Structures of the left palpus are depicted. All morphological measurements are given in millimetres. Somatic morphology measurements were taken using a scale reticule in the eyepiece of the stereo microscope. Measurements of the legs are taken from the dorsal side. Spines on leg segments are listed in the following order: dorsal-prolateral-retrolateral-proventral-retroventral.

Male palps were detached and transferred to glycerol for examination under the microscope. Female genitalia were excised using sharpened needles and then transferred to clove oil for examination under the microscope. Later, palps and epigynes were returned to 70% ethanol.

Type material and important reference material is deposited in the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, the other material is deposited in the collections of the individuals listed below.

The following abbreviations are used in the text:
AME: anterior median eyes;
CJVK: collection Johan Van Keer;
CHDK: collection Herman De Koninck;
CRB: collection Robert Bosmans;
KBIN: Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels);
Legs: Ta: tarsus; Mt: metatarsus; Pa: patella; Fe: femur.
Spines: d: dorsal; v: ventral; pl: prolateral; rl: retrolateral; spines listed between brackets: occurring in pairs or groups at about the same level; *: spines with a terminal position.

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submitted: 14.1.2010, accepted: 11.5.2010; online: 10.1.2011

Results

Family Agelenidae

Genus *Tegenaria* Latreille, 1804

According to BOLZERN et al. (2009), the differences between the genera *Tegenaria* and *Malthonica* Simon, 1898 remain unclear. GUSEINOV et al. (2005) distinguished the two genera by the embolus length but BOLZERN et al. (2008) argued that this character is unsuitable for phylogenetic evaluation. Assigning a new species to a correct genus thus becomes difficult without a comprehensive revision of the two genera (BOLZERN et al., 2009). The species described below has a relatively short embolus and is provisionally placed in the genus *Tegenaria*.

Tegenaria maelfaiti sp. nov. (Figs. 1-5).

Type material. Holotype male, 2 paratype males from Greece, Lesbos, Nomos Mandamados: road Klio-Sykaminia (N 39°22'33" E 26°10'59"), 350 m, litter and stones in small *Pinus* forest, 27.III.2008, R. Bosmans leg.; paratype female from Greece, Lesbos, Nomos Agiasos, Agiasos S. (N 39°05'53" E 26°21'57"), 550 m, stones in *Castanea* forest, 2.IV.2008, L. Baert leg. (KBIN). Deposited in KBIN.

Etymology: The species is dedicated to my good friend and excellent ecologist the late Jean-Pierre Maelfait.

Diagnosis: Males of the species are readily distinguished from other *Tegenaria* species by the combined characters of the tibial apophyses and the bifid median apophyses. *Tegenaria longimana* Simon, 1879 from Turkey is a related species, with similar but differently shaped tibial apophysis and distal parts of the median apophysis. Females are recognized by the absence of sclerotisation in the epigyne and the course of the copulatory ducts.

Description

Measurements (males n=27, females n=4): Male: Total length 3.8-6.2; prosoma 1.59-2.79 long, 1.46-2.06 wide. Female: Total length 4.8-5.0; prosoma 1.87-1.98 long, 1.34-1.43 wide. Leg measurements as in Table 1.

Table 1: *Tegenaria maelfaiti* sp. nov. leg measurements (holotype).

	Fe	Pt	Ti	Mt	Ta
Palp	1.23	0.42	0.76	-	0.79
I	3.24	0.92	3.29	3.44	1.62
II	2.85	0.78	2.31	2.97	1.37
III	3.23	0.60	1.96	2.57	0.96
IV	2.96	0.76	2.72	3.52	3.51

Colour: Prosoma yellowish brown to brown, with submarginal stripe, touching at level of fovea, and narrow grey margin; chelicerae yellowish brown; sternum grey with median stripe and 3 lateral whitish spots. Legs pale yellowish, Fe, Ti and Mt greyish at ends, Fe with 2 grey annulations, Ti and Mt with 1 median annulation. Abdomen dorsally greyish black, with anteromedian area and 5-6 chevrons whitish, ventrally whitish with scattered greyish black spots, anastomising in some specimens. Spinnerets whitish, dorsal side of dorsal spinneret and ventral side of ventral spinneret greyish black. Leg spination as in Table 2.

Male palp (Figs. 1-3): Tibia elongated, dorsal apophysis long, with parallel margins and rounded terminally, retrolateral apophysis a large, rounded lobe. Median apophysis bifid, with shorter, pointed anterior tooth and longer, less pointed posterior tooth. Conductor slightly shorter than alveolus, rounded, folded along its entire retrolateral margin, terminal part pointing in posterior direction. Embolus filiform, semi-circular, arising on mesal side of bulbus.

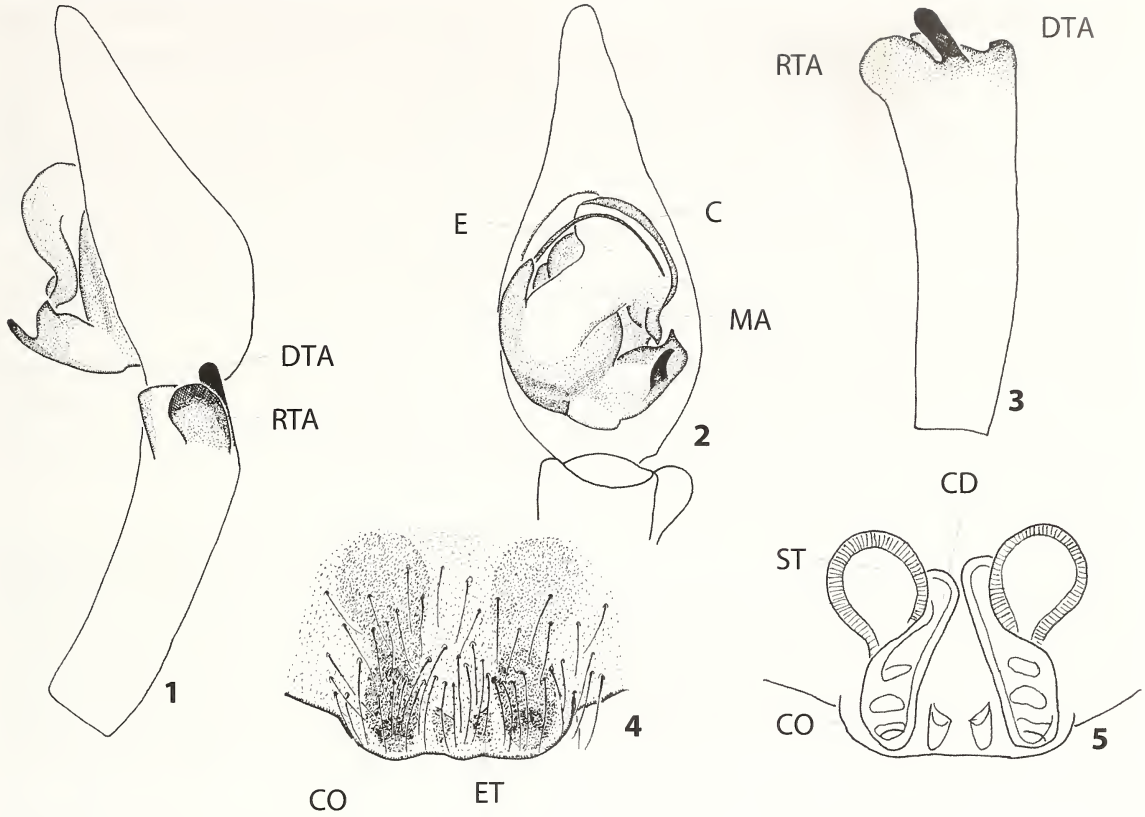
Epigynum and vulva (Figs. 4-5): Epigynal plate slightly protruding over epigastric furrow, posterior margin with two indistinct concavities, with a pair of posteriorly directed teeth but without exterior sclerifications; copulatory ducts wide; spermathecae rounded.

Further material examined

Agiasos: Oros Olympos (N 39°04'01" E 26°21'30"), 800 m, 1 female, stones in *Platanus* forest, 2.VI.2008 (CRB); - Kalloni: Anemotia, E. of Moni Voukolon (N 39°04'00" E 26°07'18), 400 m, 1 female, stones in grassland, 29.III.2008 (KBIN); road Anemotia-Skala Kallonis, Karyo (N 39°13'36" E 26°07'50"), 100 m, litter and herbs along rivulet, 29.III.2008 (CRB); - Mandamados: road Klio-Sykaminia (N 39°22'33" E 26°10'59"), 350 m, 24 males, litter and stones in small *Pinus* forest, 27.III.2008 (CHDK, CJVK, CRB); - Mithymna: road Argenos-Vafios (N 39°21'06" E

Table 2: *Tegenaria maelfaiti* sp. nov. leg spination (holotype).

	Fe	Pt	Ti	Mt	Ta
I	(dpl)-d-pl	d-d	d	v rl (plrl)	-
II	d-d-(plrl)	d-d	d	vpl 2v (plrl)	-
III	d-d-(plrl)	d-d	d (plrl)	rl pv (rlplpvrv)	-
IV	d-(pl-rl)	d-d	(drl) (pvplrl) (dplrl)	(pvrv) (plrlrv) (plrlpvrv)	-



Figures 1-5: *Tegenaria maelfaiti* sp. nov. 1. Male palp, lateral view; 2. Idem, ventral view; 3. Palpal tibia, dorsal view; 4. Epigyne, ventral view; 5. Vulva, ventral view. C = conductor; CD = copulatory duct; CO = copulatory opening; DTA = dorsal tibial apophysis; E = embolus; ET = epigynal tooth; MA = median apophysis; RTA = retrolateral tibial apophysis; ST = spermatheca.

26°14'29"), 320 m, 3 males, stony grassland and shrubs, 28.III.2008 (CHDK, CJVK, CRB).

Ecology: Males were collected in March and April, females in March, April and June. It was mainly found in forest (pine, chestnut and plane forests), but also in shrubs and olive groves and along rivulets.

Distribution: Only known from Lesbos. As *Tegenaria* species tend towards small distribution areas, this species is possibly endemic to the island.

Family Amaurobiidae

Genus *Amaurobius* C. L. Koch

The genus *Amaurobius* currently includes 67 species (PLATNICK 2010) and has a mainly Holarctic distribution. In Greece, it has been thoroughly studied by THALER & KNOFLACH (1991, 1993, 1995, 1998, 2002) and WUNDERLICH (1995). Thirteen *Amaurobius* species have been found in Greece (BOSMANS & CHATZAKI 2005). *A. candia* Thaler & Knoflach, 2002, *A. cretaensis* Wunderlich, 1995 and *A. geminus* Thaler & Knoflach, 2002 are endemics for Crete, *A. phaeacus* Thaler & Knoflach, 1998 is an endemic for Kerkyra, *A. deelemanae* Thaler & Knoflach, 1995 occurs on Crete, the Dodekanisa and Kyklades and *A. ausobskyi* Thaler & Knoflach, *A. longipes* Thaler & Knoflach, 1995, *A. ossa* Thaler & Knoflach, 1993, *A. paon* Thaler & Knoflach, 1993 and *A. pelops* Thaler & Knoflach, 1991 are endemics occurring in continental Greece. *Amaurobius pallidus* L. Koch, 1868 and *A. strandi* Charitonov, 1937 have an eastern Mediterranean distribution and *A. erberi* (Keyserling, 1863) has a circummediterranean distribution. From the Eastern Aegean islands (to which Lesbos belongs) only *Amaurobius scopolii* Thorell, 1871 has been cited from Chios (STRAND 1917) but this is most probably a misidentification. It is thus not surprising to discover another new *Amaurobius* species on one of the Aegean Islands.

Amaurobius lesbius sp. nov. (Figs. 6-10)

Type material: Holotype male, 1 paratype male two paratype females from Greece, Lesbos, Nomos Kalloni, Skalochori (N 39°15'59" E26° 05' 30"), 300 m, litter in *Quercus* forest, 2.X.2007, R. Bosmans & J. Van Keer leg. Deposited in KBIN.

Etymology: The species is named after the island of Lesbos.

Diagnosis: *Amaurobius lesbius* n. sp. is closely related to the larger *A. erberi* (Keyserling), also occurring on Lesbos. Males differ by the reduction of an intermediate apophysis in the palpal tibia, and the presence of a strongly protruding, rectangular tegular process. Females differ by the closely set spermathecae, separated by less than ¼ their diameter in the new species and by their diameter in *A. erberi*.

Description

Colour: Prosoma yellowish brown, sometimes with greyish striae, thoracic part paler; chelicerae dark orange brown. Legs yellowish brown. Abdomen in males dark grey to black with anteromedian pale stripe and some subterminal, pale grey chevrons, venter pale to dark grey, in females dorsally pale grey with dark grey pattern.

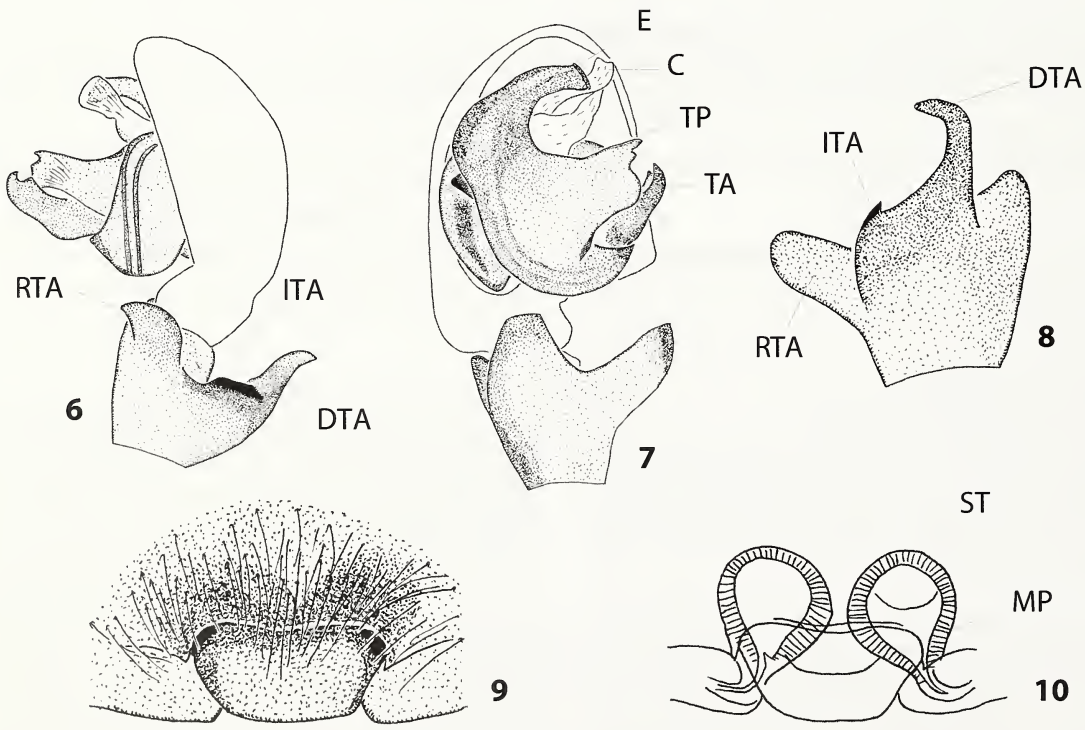
Measurements (males: n=6; females: n= 8): Male: Total length 3.6-4.6; prosoma 1.81-2.24 long, 1.21-1.56 wide. Female: Total length 4.8-6.8; prosoma 1.99-2.26 long, 1.18-1.54 wide. Leg measurements as in Table 3, leg spination as in Table 4.

Male palp (Figs. 6-8): Tibia with small, curved dorsal and larger blunt retrolateral apophyses, the former with a tooth at its base, intermediate apophysis reduced to a short crest. Tegular process strongly protruding, nearly rectangular. Tegular apophysis elongated, terminally hooked and embolus short and bent.

Epigyne and vulva (Figs. 9-10): With reversed tra-

Table 3: *Amaurobius lesbius* sp. nov., leg measurements (holotype).

	Fe	Pt	Ti	Mt	Ta
Palp	0.72	0.26	0.34	-	0.39
I	1.51	0.76	1.36	1.54	0.91
II	1.42	0.74	1.14	1.08	0.89
III	1.31	0.75	0.99	1.29	0.77
IV	2.02	0.79	1.82	2.28	1.12



Figures 6-10: *Amaurobius lesbius* sp. nov. 6. Male palp, lateral view; 7. Idem, ventral view; 8. Palpal tibia, dorsal view; 9. Epigyne, ventral view; 10. Vulva, ventral view. C = conductor; DTA = dorsal tibial apophysis; E = embolus; ITA = intermediate tibial apophysis; MP = median plate; RTA = retrolateral tibial apophysis; ST = spermatheca; TA = tegular apophysis; TP = tegular process.

Table 4: *Amaurobius lesbius* sp. nov., leg spination (holotype).

	Fe	Pt	Ti	Mt	Ta
I	pl	-	3pl 2rl 3pv 3rv	2pl 2rl 3pv 3rv pdrd*	-
II	pl	-	3pl 2rl 3pv 3rv	3pl 2rl pv 2rv pdrd*	-
III	(pd rd)	-	3pl 3pv rv rl	2pl pv 3rv pd rd*	-
IV	rd	-	pv 3rv rl	rl pv 3rv pd pv*	-

pezoid plate. Spermathecae closely set, separated by less than ¼ their diameter, basal part covered by epigynal plate.

Further material examined
Agiasos: Agiasos S. (N 39°05'53" E 26°21'57"), 550 m, 5 males, pitfalls in *Castanea* forest, X.2007-IV.2008 (CJVK); - Mandamados: road Klio-Sykaminia (N 39°22'33" E 26°10'59"), 350 m, stones in small *Pinus* forest, 1 subadult male 1 female, 6.X.2007, 6 females, 27.III.2008 (CHDK, CJVK, CRB).

Ecology: All specimens were captured in *Castanea*, *Pinus* and *Quercus* forests. Males were only collected in winter, females in winter and spring.

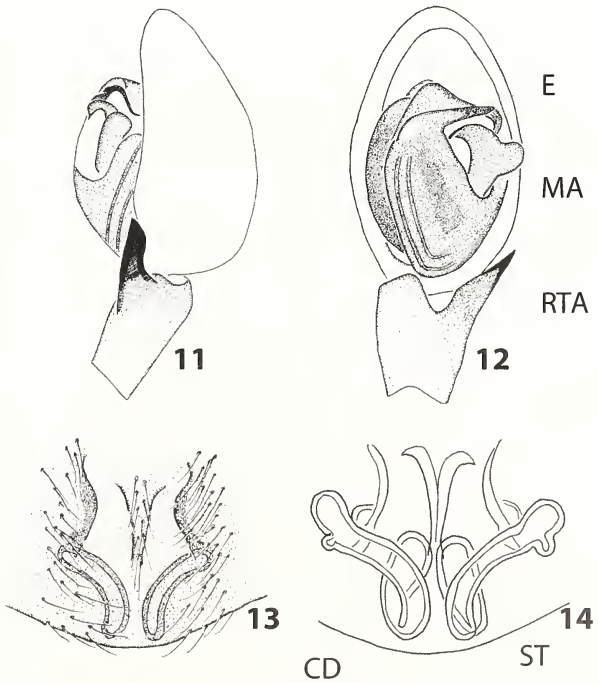
Distribution: At the moment, the species is only known from Lesbos, but as *Amaurobius* species generally have large distribution areas, it may occur on other East Aegean Islands as well.

Family Liocranidae
Genus *Agroeca* C. L. Koch
The genus *Agroeca* currently includes 25 species and has a Holarctic distribution (PLATNICK 2010). In Greece, only *Agroeca cuprea* Menge, 1873 has been previously reported (BOSMANS & CHATZAKI 2005). A new species is described below.

Agroeca parva sp. nov.
(Figs. 11-14)
Type material: Holotype male, 2 male paratypes 1 female paratype from Greece, Lesbos, Polichnitos, Aghios Pavlos E. (N 39°07'38" E 26°14'03"), 10 m, pitfalls in *Juncus* marsh, 11.X.2007, R. Bosmans leg. Deposited in KBIN.

Etymology: The name refers to the small size of the new species.
Diagnosis: *Agroeca parva* sp. nov. is recognised by its small size and its contrasting colour. The male palp and female epigyne suggest the species is closely related to *Agroeca annulipes* Simon, 1878 and *A. maghrebensis* Bosmans, 1999, both from the western Mediterranean. Males differ by the truncate palpal tibial apophysis, more pointed in the species from the Maghreb, females by the concave lateral margins of the epigynal depression, straight in the species from the Maghreb.

Description
Colour: Prosoma yellowish brown with narrow margin and submedian stripe greyish black. Abdomen grey black, median denticulate stripe grey brown, venter yellowish brown with few grey black spots in posterior half. Legs yellowish brown, femora with 2 broad grey annulations, patellae I-III with basal half grey.
Measurements (males: n =3, females n = 6)**:** Male: Total length 3.6-3.8; prosoma 1.84-2.12 long, 1.44-1.71 wide. Female: Total length 4.1-4.5; prosoma 1.83-2.16 long, 1.51-1.64 wide. Leg measurements as in Table 5, leg spination as in Table 6.



Figures 11-14: *Agroeca parva* sp. nov. 11. Male palp, lateral view; 12. Idem, ventral view; 13. Epigyne, ventral view; 14. Vulva, ventral view. CD = copulatory duct; E = embolus; MA = Median apohysis; RTA = retrolateral tibial apophysis; ST = spermatheca.

Table 5: *Agroeca parva* sp. nov. leg measurements (holotype).

	Fe	Pt	Ti	Mt	Ta
Palp	0.72	0.26	0.34	-	0.39
I	1.51	0.76	1.36	1.54	0.91
II	1.42	0.74	1.14	1.08	0.89
III	1.31	0.75	0.99	1.29	0.77
IV	2.02	0.79	1.82	2.28	1.12

Table 6: *Agroeca parva* sp. nov. leg spination (holotype).

	Fe	Pt	Ti	Mt	Ta
I	2d 1pl	-	2 (pv rv)	3 (pv rv)	-
II	2d 1pl	-	2 (pv rv)	3 (pv rv)	-
III	2d 1pl	1d	2pl 3pv 3rv 2rl	3 pl 3pv 3rv 3rl	-
IV	2d 1pl	1d	3pl 3pv 3pl 3rl	3 pl 3pv 3rv 3rl	-

Male palp (Figs. 11, 12): Tibia with thick, straight apophysis, terminally truncate at dorsal margin. Median apophysis reversed L-shaped, with distinct anterior concavity and terminally pointed. Embolus gradually narrowing terminally curved towards the median apophysis.

Epigyne and vulva (Figs. 13-14): With large median depression, concave lateral margins and a posteriorly narrowing median septum.

Further material examined

Agiasos: Megali Limni W., Steni Klidi, (N 39°06'47" E 26°18'30"), 400 m, 2 females, pitfalls in *Pinus* forest, 3.IV.2008 (CJVK, CRB); - Kalloni: Skala Kalloni (N 39°12'28" E 26°12'01"), 10 m, 1 female, litter in vegetable garden of hotel, 6.X .2007 (CRB); - Polichnitos: Polichnitos salt works (N 39°06'37" E 26°10'50"), 5 m, stones in *Salicornia* salt marsh, 2 females, 31.III.2008 (CRB); Vatera (N 39°01'00" E 26°13'59"), 30 m, 1 male, litter in garden of hotel, 9.X.2007 (CRB).

Ecology: Males of this species were only collected in October, females in October and March. It was found in salt marshes, pine forests and even in a vegetable garden, so there seem to be no particular habitat preferences.

Distribution: Currently, only known from Lesbos, but as all other *Agroeca* species have large distribution areas, it probably occurs in a much wider area.

Family Corinnidae

Genus *Arabelia* Bosselaers, 2009

The genus *Arabelia* was only recently described and includes a single species from the East Mediterranean region. The male is described here for the first time.

***Arabelia pheidoleicomes* Bosselaers, 2009**

(Figs. 15-16)

Arabelia pheidoleicomes Bosselaers, 2009: 51, Figs. 2K, 7 A-G, 8H, 9 (descr. female).

Remark

The female of this species was recently described by BOSSELAERS (2009), based on material from Rhodes and Lesbos. Later, the corresponding male appeared to be present in the material from Lesbos as well and it is described here for the first time. Somatic morphology is the same as in the female, except as indicated below.

Diagnosis

The male of this species is recognised by the short, pointed tibial apophysis and the small sperm duct tooth. For a description of the female, see BOSSELAERS (2009).

Description of the unknown male

Colour: As in female, but femora and patella of legs I-II somewhat infuscate, contrasting with paler remaining segments.

Measurements (1 male): Total length 3.5; prosoma 1.36 long, 1.21 wide. Leg measurements as in Table 7, leg spination as in Tab. 8.

Male palp (Figs. 15-16): Tibia with small, pointed retrolateral apophysis. Bulbus ovoid, without apophyses, only with small, anterolateral sperm duct tooth.

Material examined

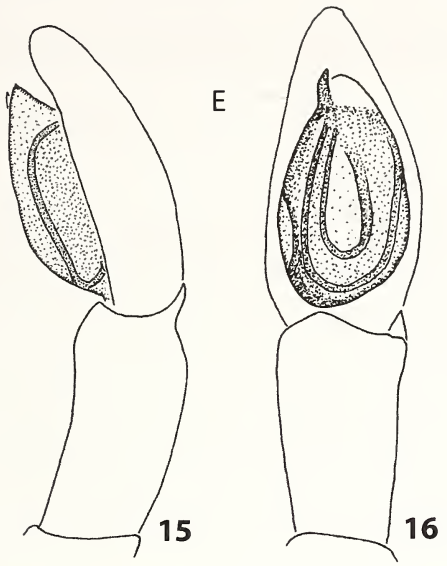
Agiasos: Agiasos NW, Voula (N 39°06'26" E 26°21'14"), 350 m, 1 male, 1.IV.2008, dense *Pinus* forest along rivulet, 1.IV.2008, L. Baert leg.; deposited in KBIN.

Distribution

Greece (Rhodes, Lesbos) and Cyprus.

Ecology

Females were always collected together with ants, the only male collected was found in a termite nest.



Figures 15-16: *Arabelia pheidoleicomes* Bosselaers, 2009. 15. Male palp, lateral view; 16. Idem, ventral view. E = embolus.

New spider records from Lesbos

Fam. Gnaphosidae

***Drassodes lacertosus* O. P.-Cambridge, 1872**

Identification

Levy, 2004: 6, f. 13-19.

Material examined

Mithymna: Mithymna (N 39°22'02" E 26°10'30"), 10 m, 1 male in pool of hotel, 28.V.2009, A. Decae leg. (CRB).

Distribution: The species is known from Turkey, Israel, Syria and Russia (PLATNICK 2010) and is new to Greece. The present record is the most western one.

***Trachyzelotes barbatus* (L. Koch, 1866)**

Identfication

Chatzaki, Thaler & Mylonas, 2003: 53, f. 20-21, 26-27.

Material examined

Mithymna: Mithymna (N 39°22'02" E 26°10'30"), 10 m, 4 males 1 female in pool of hotel, 28.V.2009, A. Decae leg. (CRB).

Distribution: Mediterranean to Central Asia, USA. New to Lesbos, but previously recorded in continental Greece and Crete (CHATZAKI et al. 2003).

Discussion

In their catalogue of the spiders of Lesbos, BOSMANS et al. (2009) list 298 species, some of them previously undescribed. Three *Harpactea* species and one *Stalagtia* species were described in VAN KEER & BOSMANS (2009), one *Zodarion* species in BOSMANS (2009) and three more species are described in the present paper. Additional species belonging to the spider family Linyphiidae will be described in a further paper.

Finally, some species were discovered that remain unidentified to species level, for different reasons. Sometimes, only one sex was captured, sometimes the genus is in need of revision or the systematic position is unclear. Further investigations are necessary to solve these problems. The description of these species can only be carried out after revisions of the relevant genera or after the discovery of the corresponding sex.

Acknowledgements

I wish to thank my friends and colleagues Léon Baert, Jan Bosselaers, Herman De Koninck, Jean-Pierre and Lutgarde Maelfait and Johan Van Keer for joining me on Lesbos and making this journey such a pleasant event and also allowing me to examine their material. Arthur Decae is thanked for making available his material collected in Lesbos. The English of the final draft was kindly checked by Anthony Russell-Smith.

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Arachnologische Mitteilungen 40: 23-32 Nuremberg, January 2011

The faunistic diversity of cave-dwelling spiders (Arachnida, Araneae) of Greece

Christo Deltshev

doi: 10.5431/aramit4004

Abstract: Until today, from Greek caves a total of 109 species of spiders belonging to 25 families are known. One species, the linyphiid *Porrhomma convexum* (Westring, 1861) was recorded here for the first time in Greece. The 109 species are distributed in caves of different geographic territories as follows: Thrace – 8 species, Macedonia – 18, Epirus – 1, Thessaly – 6, Central Greece – 3, Attiki-Saronic Islands – 24, Peloponnese – 15, Evoia-Vories Sporades – 1, Eastern Aegean Islands – 5, Cyclades – 3, Dodecanese – 6, Ionian Islands – 23, Crete – 47. The largest fraction of troglobite species were encountered mainly in the territories of Crete – 15 species (5 of which are anophthalmic), the Ionian Islands – 4, Thrace – 2 (both anophthalmic), the Attiki-Saronic Islands – 2 (both anophthalmic), the Peloponnese – 2 (one anophthalmic), and Macedonia, Thessaly, and the Cyclades – each with 2 species. The richness of the troglobitic spiders in these regions strengthens the assumption that they were major centres of speciation and evolution for the species of this group. According to their current distribution, the established 109 species can be classified into 12 zoogeograpical categories, grouped into 4 complexes (widely distributed, European, Mediterranean, endemics). The largest number of species belong to the endemic complex (53.2 %) and are also the most characteristic and reflect the local character of the cave-dwelling spiders.

Key words: cave-spiders fauna, endemics, troglobites, zoogeography

The earliest data on Greek cave-dwelling spiders were presented by SIMON (1885), KULCZYŃSKI (1903), ROEWER (1928, 1959), DRENSKY (1936); KRATOCHVÍL (1937, 1938), HADJISSARANTOS (1940), and FAGE (1945). More recent publications derive from the investigations of BRIGNOLI (1968, 1971a, 1971b, 1972, 1974a, 1974b, 1974c, 1976, 1977, 1978, 1979, 1984), DEELEMAN-REINHOLD (1971, 1977, 1983, 1985, 1989, 1993), DEELEMAN-REINHOLD & DEELEMAN (1988), SENGLET (1971, 2001), DELTSHEV (1979, 1985, 1999, 2000, 2008), BERON (1985, 1986), BERON & STOEV (2004), THALER & KNOFLACH (1995), WUNDERLICH (1995), BOSSELAERS (1998), BOSSELAERS & HENDERICKX (2002), GASPARO (2003, 2004a, 2004b, 2005a, 2005b, 2006, 2007, 2008, 2009), CHATZAKI et al 2002, BOSMANS & CHATZAKI (2005), CHATZAKI & ARNEDO (2006), and PLATNICK (2009). The critical incorporation of all available literature records and the accumulation of new data are now sufficient to allow a critical analysis of the distribution of spiders established in the caves of Greece.

Study area and material

Greece is a country in south-eastern Europe, situated on the southern end of the Balkan Peninsula. The country has borders with Albania, the Republic of Macedonia and Bulgaria to the north, and Turkey to the east. The Aegean Sea lies to the east and south of mainland Greece, while the Ionian Sea lies to the west. Both parts of the Eastern Mediterranean basin feature a vast number of islands, islets and rock islands (Fig.1). Two-thirds of the territory of Greece is dominated by limestone, many of which are karstified (CLENDENON 2009).

The territory of Greece can be divided into 13 geographical regions (BOSMANS & CHATZAKI 2005; Fig. 1). There are 7 geographical regions on the mainland: Thrace, Macedonia, Epirus, Thessaly, Central Greece, Attica and the Peloponnese. The Ionian Islands are situated on the western border of Greece in the Ionian Sea. There are several island groups in the Aegean Sea on the eastern side of Greece: Evoia and the Sporades, the Saronic Islands (grouped with Attica), the Cyclades, the Eastern Aegean Islands, the Dodecanese and Crete (Fig. 1).

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submitted: 30.12.2010, accepted: 9.4.2010; online: 10.1.2011

Results

Species composition

The spiders established in the caves of Greece (Mainland and Insular part) are represented by 109 species, included in 52 genera and 25 families: Ctenizidae – 1, Filistatidae – 1, Sicariidae – 1, Scytodidae – 1, Leptonetidae – 9, Pholcidae – 10, Segestriidae – 3, Dysderidae – 12, Oonopidae – 1, Mimetidae – 1, Ere-

Figure 1: Map of different geographical regions in Greece.

sidae – 1, Uloboridae – 1, Nesticidae – 4, Theridiidae – 4, Anapidae – 1, Linyphiidae – 16, Tetragnathidae – 4, Araneidae – 1, Lycosidae – 1, Agelenidae – 21, Amaurobiidae – 4, Gnaphosidae – 6, Philodromidae – 1, Thomisidae – 2, Salticidae – 2 (Table 1). One species is new for the Greek spider fauna: *Porrhomma convexum* (Westring, 1861) (marked in the list with *), a spider with a Holarctic distribution and widespread in European caves. It is also well represented in the caves of the Balkan Penisula – and not only established in the caves of Croatia, Romania and Turkey (DELTSHEV 2008). The number of species is high and represents about 13 % of the Greek spiders. This is also evident from a comparison with the number of cave-dwelling spiders recorded from the other countries of the Balkan Peninsula: Bulgaria – 99, Croatia – 63, Serbia – 59, Bosnia and Herzegovina – 52, Macedonia – 44, Montenegro – 44, Slovenia – 43, Albania – 10, Turkey – 8, and Romania – 4 (DELTSHEV 2008). The established number of species, however, depends not only on the size of the regions, but also on the degree of exploration. The most characteristic are the families: Leptonetidae (8.2 %), Pholcidae (9.2 %), Dysderidae (11 %), Linyphiidae (14.6 %), and Agelenidae (19.2 %). The families with largest number of anophthalmic species are Leptonetidae (6), Dysderidae (3), Nesticidae (2), and Linyphiidae (1). The genera with the largest number of species are *Tegenaria* (8), *Lepthyphantes* (6), *Harpactea* (5), and *Histopona* (5).

The species are distributed in caves belonging to the geographic territories of Greece as follows: Thrace – 8 species, Macedonia – 18, Epirus – 1, Thessaly – 6, Central Greece – 3, te Attiki-Saronic Islands – 24, the Peloponnese – 15, Evoia-Voroies Sporades – 1, the Eastern Aegean Islands – 5, the Cyclades – 7, the Dodecanese – 6, the Ionian Islands – 23, Crete – 47 (Table 1). We also have to emphasise that the degree of exploration in these territories is not equal: the territories of Evoia-Sporades, the Cyclades, the Dodecanese and Central Greece are less explored.

Cave-dwelling spiders can be categorised into four ecological groups (SKET 2008):

- troglobites: species limited to a life cycle in caves. Often they show a suite of characters, associated with their adaptation to subterranean life: loss of pigment, loss of eyes and elongation of appendages.
- eutroglophiles: species which can live their entire life in caves, but also occur in other environments.
- subtroglophiles: species which utilise caves, but must leave the caves to complete their life cycle.
- trogloxenes: species which occur underground sporadically.

The largest fraction of troglobite species was encountered mainly in the caves of the territories of Crete –15 (5 anophthalmic), the Ionian Islands – 4, Thrace – 2 (2 anophthalmic), the Attiki-Saronic Islands 2 (2 anophthalmic), the Peloponnese – 2 (1 anophthalmic), and Macedonia, Thessaly and the Cyclades each by 2 species (Table 1). All troglobites are endemics for the territory of Greece or the Balkan Peninsula.

Very important is the presence of eutroglophiles (35 species), because together with troglobites (29 species), they can be considered as dependent faunistic elements of caves. The largest number of species is established in the caves of Crete (14 species), the Ionian Islands (11 species), the Attiki-Saronic Islands (9 species), Macedonia (8 species), and the Peloponnese (8 species). Here, the endemics are represented by 14 species (35 %). A present day example of active subterranean colonisation and cave penetration are the species *Lepthyphantes centromeroides* and *Palliduphantes spelaeorum*, widespread in the Balkan Peninsula (DEELEMAN-REINHOLD 1978). Here, the species *Palliduphantes istrianus* should also be included.

Table 1: Species composition of cave dwelling spiders in Greece

Category (CAT): tb – troglobite; **tba** – troglobite anophtalmic; **etph** – eutroglophile; **stph –** subtroglophile; **tx -** trogloxene

Zoogeography (Z_G): COS – Cosmopolitan; **H –** Holarctic; **P** - Palearctic; **WP** - West Palearctic; **ECA** - European-Central Asian; **E** - European; **MSEE** - Middle Southeast European; **MCA** – Mediterranean-Central Asian; **M** - Mediterranean; **NM** - North Mediterranean; **NEM** - Northeast Mediterranean; **E –** Endemics; **ETHR -** Endemic for Thrace; **EMTH -** Endemic for Macedonia and Thrace; **EEP** - Endemic for Epirus; **EETI** - Endemic for Epirus, Thessaly and Ionian Islands; **ECGR -** Endemic for Central Greece; **EAS -** Endemic for Attiki-Saronic Islands; **ECOG –** Endemic for continental Greece**; EPE -** Endemic for Peloponese; **EAP** - Endemic for Attiki-Saronic Islands and Peloponese; **EPI –** Endemic for Peloponnisus and Ionian Islands; **EEAI -** Endemic for Eastern Aegean Islands; **ECY -** Endemic for Cyclades; **EKA -** Endemic for Karpathos; **EIO -** Endemic for Ionian Islands; **ECR –** Endemic for Crete; **EGR** - Endemic for continental and island Greece; **EBP -** Endemic for Balkan Peninsula.

Distribution: THR – Thrace**; MA –** Macedonia; **EP –** Epirus; **THE –** Thessaly; **CGR –** Central Greece; **ASI -** Attiki-Saronic Islands; **PE –** Peloponnese; **ESI -** Evia-Sporades; **EAI -** Eastern Aegean Islands; **CY -** Cyclades; **DO –** Dodecanese**; IO –** Ionian Islands; **CR –** Crete.

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Cyrtaucheniidae															
Cyrtocarenum grajum (C.L. Koch 1836)	tx	ECR													x
Filistatidae															
Filistata insidiatrix (Forsskål, 1775)	stph	M		x										x	x
Sicaridae															
Loxosceles rufescens (Dufour, 1820)	stph	COS		x				x	x				x		x
Scytododae															
Scytodes thoracica Latreille, 1804	stph	H							x				x	x	x
Leptonetidae															
Barusia laconica (Brignoli, 1974)	tb	EPE							x					x	
Cataleptoneta sengleti (Brignoli, 1974)	tba	ECR													x
Leptonetela andreevi Deltshev, 1985	tba	ECY													
Leptonetela kanellisi (Deeleman-Reinhold, 1971)	tba	EAS						x							
Leptonetela strinatii (Brignoli, 1976)	tba	EAS						x							
Leptonetela thracia Gasparo, 2005	tba	ETHR	x												
Sulcia cretica cretica Fage, 1945	tb	ECR													x
Sulcia cretica lindbergi Dresco, 1962	tba	EEP			x										x
Sulcia cretica violacea Brignoli, 1974	tb	EETI			x	x								x	
Pholcidae															
Holocnemus pluchei (Scopoli, 1763)	etph	M		x				x					x	x	x
Hoplopholcus figulus Brignoli, 1971	etph	EEAI									x				
Hoplopholcus labyrinthi (Kulczyński, 1903)	tb	ECR													x
Hoplopholcus minotaurinus Senglet, 1971	tb	ECR													x
Hoplopholcus minous Senglet, 1971	stph	EKA											x		
Pholcus creticus Senglet, 1971	etph	ECR													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Pholcus opilionoides (Schrank, 1781)	etph	H													x
Pholcus phalangioides (Fuesslin, 1775)	etph	COS		x								x			x
Spermophora senoculata (Dugès, 1836)	etph	H											x		
Stygopholcus photophilus (Senglet, 1971)	etph	EGR		x		x					x			x	x
Segestridae															
Segestria florentina (Rossi, 1790)	tx	WP						x							x
Segestria sbordonii Brignoli, 1984	tx	ECR													x
Segestria senoculata (Linnaeus, 1758)	tx	P												x	
Dysderidae															
Dysdera cephalonica Deeleman-Reinhold, 1988	tx	EIO											x		
Dysdera crocata C.L. Koch, 1838	etph	COS													x
Dysderocrates gasparoi Deeleman-Reinhold, 1988	etph	EIO												x	
Dysderocrates marani (Kratochvíl, 1937)	etph	ECR													x
Harpactea catholica (Brignoli, 1984)	etph	ECR													x
Harpactea corinthia Brignoli, 1984	etph	EPE							x						
Harpactea loebli Brignoli, 1974	tx	EIO												x	
Harpactea rubicunda (C.L. Koch, 1838)	stph	E	x	x											
Harpactea strinatii Brignoli, 1979	tba	EPE							x						
Minotauria attemsi Kulczyński, 1903	tb	ECR													x
Minotauria fagei (Kratochvíl, 1970)	tba	ECR													x
Rhodera hypogea Deeleman-Reinhold, 1989	tba	ECR													x
Oonopidae															
Oonops mahnerti Brignoli, 1974	tx	EPE							x						
Mimetidae															
Ero flammeola Simon, 1881	tx	M												x	
Eresidae															
Eresus kollari Rossi, 1846	tx	ECA						x	x						
Uloboridae															
Uloborus plumipes Lucas, 1846	tx	COS						x					x		
Nesticidae															
Nesticus beshkovi Deltshev, 1979	tba	ECR													x
Nesticus cellulanus (Clerck, 1757)	etph	H		x											
Nesticus eremita Simon, 1879	tb	NEM				x				x				x	
Nesticus henderickxi Bosselaers, 1998	tba	K													x
Theridiidae															
Crustulina scabripes Simon, 1881	tx	M											x		
Steatoda castanea (Clerck, 1757)	tx	P													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Steatoda grossa (C.L. Koch, 1838)	stph	COS												x	x
Steatoda triangulosa (Walckenaer, 1802)	stph	COS							x						
Anapidae															
Zangherella apuliae (Caporiacco, 1949)	tb	NM												x	
Linyphiidae															
Centromerus milleri Deltshev, 1974	tba	EMTH	x												
Diplocephalus turcicus Brignoli, 1972	tx	NEM						x							
Icariella hauseri Brignoli, 1979	tx	EGR									x				
Lepthyphantes beroni Deltshev, 1979	tb	ECR										x			x
Lepthyphantes beshkovi Deltshev, 1979	tb	ECR													x
Lepthyphantes brignolianus Deltshev, 1979	tb	ECR													x
Lepthyphantes kratochvili Fage, 1945	tb	ECR													x
Lepthyphantes magnesiae Brignoli, 1979	etph	ECOG							x						
Palliduphantes byzantinus (Fage, 1931)	etph	EBP							x						
Palliduphantes epaminondae (Brignoli, 1979)	tb	ECGR					x								
Palliduphantes istrianus (Kulczyński, 1914)	tb	EBP		x										x	
Palliduphantes spelaeorum (Kulczyński, 1914)	tb	EBP		x											
Porrhomma convexum (Westring, 1851)	tb	P		x											
Savignia naniplopi Bosselaers & Henderickx, 2002	tx	ECR													x
Tenuiphantes tenuis (Blackwall, 1852)	tx	E												x	
Tetragnathidae															
Meta bourneti Simon, 1922	etph	WP	x					x	x						
Meta menardi (Latreille, 1804)	etph	E				x		x	x						
Metellina merianae (Scopoli, 1763)	etph	E		x				x						x	x
Tetragnatha montana Simon, 1874	tx	P		x											
Araneidae															
Larinioides suspicax (O.P.-Cambridge, 1876)	tx	E													x
Lycosidae															
Alopecosa albofasciata (Brullé, 1832)	tx	M		x				x							x
Agelenidae															
Allagelena gracilens (C.L. Koch, 1841)	tx	WP						x							
Histopona hauseri Brignoli, 1972	etph	EIO												x	
Histopona isolata Deeleman-Reinhold, 1983	tb	ECR													x
Histopona myops (Simon, 1885)	etph	ECOG				x			x						
Histopona strinatii (Brignoli, 1976)	etph	EP							x						
Histopona thaleri Gasparo, 2005	etph	ECGR					x								
Maimuna cretica (Kulczyński, 1903)	stph	EK													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Maimuna vestita (C.L. Koch, 1841)	stph	NEM		x				x							
Malthonica dalmatica (Kulczyński, 1906)	etph	NEM									x			x	x
Malthonica ferruginea (Panzer, 1804)	etph	E	x	x				x							x
Malthonica pagana (C.L. Koch, 1840)	etph	MCA						x				x			x
Tegenaria silvestris (L. Koch, 1872)	etph	E						x							
Tegenaria achaea Brignoli, 1977	etph	EEAI									x				
Tegenaria ariadnae Brignoli, 1984	etph	ECR													x
Tegenaria domestica (Clerck, 1757)	etph	COS		x				x	x					x	
Tegenaria hauseri Brignoli, 1979	etph	EIO												x	
Tegenaria labyrinthi Brignoli, 1984	stph	ECR													x
Tegenaria paragamiani Deltshev, 2008	etph	ETHR													
Tegenaria parietina (Fourcroy, 1785)	etph	WP						x				x		x	x
Tegenaria pieperi Brignoli, 1979	tb	ECR													x
Tegenaria schmalfussi Brignoli, 1976	tb	ECR													x
Amaurobiidae															
Amaurobius cretaensis Wunderlich, 1995	tx	ECR													x
Amaurobius deelemanae Thaler & Knoflach, 1995	tx	ECDC										x			
Amaurobius pelops Thaler & Knoflach, 1991	tx	EAP						x							
Amaurobius strandi Charitonov, 1937	tx	SEE						x							
Gnaphosidae															
Drassodes lapidosus (Walckenaer, 1802)	tx	P						x							x
Nomisia ripariensis (Thorell, 1871)	tx	NEM													x
Pterotricha lentiginosa (C.L. Koch, 1837)	tx	NEM						x							x
Zelotes clivicola (L. Koch, 1870)	tx	P						x							
Zelotes femellus (L. Koch, 1866)	tx	NEM		x											
Zelotes oblongus (C.L. Koch, 1833)	tx	MSEE													x
Sparassidae															
Eusparassus walckenaeri (Audouin, 1826)	tx	NEM													x
Philodromidae															
Philodromus collinus C.L. Koch, 1835	tx	E						x							
Thomisidae															
Synema globosum (Fabricius, 1775)	tx	P						x							
Xysticus kochi Thorell, 1872	tx	WP													x
Salticidae															
Evarcha falcata (Clerck, 1757)	tx	P	x												x
Mendoza canestrinii (Ninni, 1868)	tx	P		x											

Table 2: Zoogeographical composition of cave dwelling spiders in Greece

Complexes	Chorotypes		Species	
	Classification	Code	Number	%
Widely distributed	Cosmopolitian	COS	7	6.4
	Holarctic	HOL	5	4.6
	Palearctic	PAL	9	8.2
	West Palearctic	WP	5	4.6
	European-Central Asiatic	ECA	1	0.9
	Total		**27**	**24.7**
European	European	E	8	7.3
	Middle-Southeast European	MSEE	1	0.9
	South East European	SEE	1	0.9
	Total		**10**	**9.2**
Mediterranean	Mediterranean-Central Asiatic	MCA	1	0.9
	Mediterranean	M	5	4.62
	North East Mediteranean	NEM	8	7.3
	Total		**14**	**12.8**
Endemics	Endemic for continental and island Greece	EGR	55	50.4
	Endemic for Balkan Penisnula	EBP	3	2.7
	Total		**58**	**53.2**

The group of subtroglophiles comprises 11 species occurring in dark places such as buildings, screes, rock crevices and caves. They can be considered as regular inhabitants of the caves. Three species are endemics (*Maimuna cretica*, *Hoplppholcus minous*, and *Tegenaria labyrinthi*).

The trogloxenes are represented by 36 species. They are not truly cavernicolous faunistic elements, but their presence in caves should not be ignored. On the other hand some of them will probably be considered subtroglophiles and even eutroglophiles once more information on their ecology is gathered. Here, the endemics are represented by 11 species.

Zoogeographical analysis

According to their current distribution, the established 109 species can be classified into 12 zoogeograpical categories, grouped into four complexes (widely distributed, European, Mediterranean, endemics) (Tab. 1 & 2, Fig. 2).

Best represented is the complex of endemics with 58 species (53.2 %), which include 29 troglobites, 16 troglophiles, and 12 trogloxenes. The established number is high and reflects the local character of the cave fauna. The endemics are best represented in Crete – 26 species and 2 genera (*Minotauria, Rhodera*), the Ionian Islands – 9 species, the Peloponnese – 8 species, Macedonia and the Eastern Aegean Islands – each with 4 species. The recent cave spider fauna is formed after gradual changes in the fauna of the ancient humid Tertiary forests (DEELEMAN-REINHOLD 1977). However, due to a lack of data, it is difficult to determine with certainty which cave spider endemics of the Balkans are Tertiary, and which are Quaternary, elements.

The complex of widely distributed species comprises 36 species (29.2 %). Palearctic species are dominant (47.2 %), followed by Cosmopolitan (19.4 %) Holarctic (13.8 %), West Palearctic (13.8 %), and European-Central Asiatic (5.5 %). The complex includes mostly widespread species associated with lowlands, buildings, caves, woodlands and high altitude zones of mountains. Here characteristic for caves are *Nesticus cellulanus*, *Porrhomma convexum* and *Tegenaria domestica*. These species are also largely

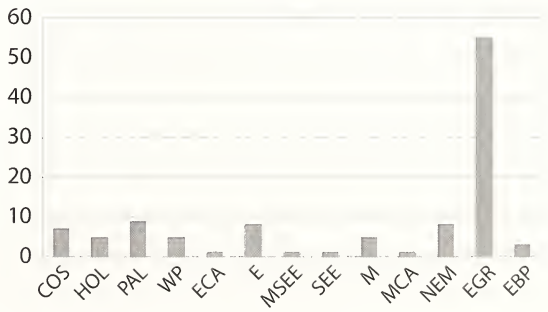

Figure 2: Relative representation of the zoogeographical categories of cave dwelling spiders in Greece (for abbreviations see Table 1).

widespread taxa in European caves where *Porrhomma convexum* occurs in the deep parts.

The European complex includes 10 species (9.2 %). European species are dominant (8 %) among this complex. The Middle Southeast European and Southeast European species are represented by single species - trogloxenes. The complex comprises widespread spiders in Europe and the Balkan Peninsula which inhabit both lowlands and mountains. The most characteristic are *Meta menardi* and *Metellina merianae*, both widespread in European caves.

The Mediterranean complex includes 14 species (12.8 %). The real representation of this category is probably higher because part of the endemic fauna has a Mediterranean origin. Dominant here are the species widespread in the Mediterranean region or part of it, but the real cavernicolous elements are *Nesticus eremita* and *Zangherella apuliae* (characteristic mainly for the superficial underground compartment) distributed in the caves of the north-west part of Greece.

Conclusions

- The faunistic diversity of the reported 109 cave-dwelling spiders shows that Greek caves are characterised by a considerable species richness. This is also supported by comparing the number of cave-dwelling spiders recorded from other countries in the Balkan Peninsula: Bulgaria – 99, Croatia – 63, Serbia – 59, Bosnia and Herzegovina – 52, Macedonia – 44, Montenegro – 44, Slovenia – 43, Albania – 10, Turkey – 8, and Romania – 4 (Deltshev 2008).
- The uneven species richness in the caves of different regions of Greece is probably due mainly to the different degree of exploration by researchers.
- Isolation and resulting endemism seems to be the driving force for the cave faunal patterns observed.
- Most characteristic, in a faunal and zoogeographical respect, is the presence of 58 endemic species in Greek caves.
- The high percentage of the endemics (53.2 %) suggests a local speciation process with consequent formation of neo-endemics.
- All troglobitic spiders are endemic, which leads to the conclusion that the regions where they are currently distributed were major centres of speciation.

Acknowledgements

We are especially grateful to our colleagues P. Beron, F. Gasparo, S. Lazarov, M. Naumova, K. Paragamian, B. Pertrov, and P. Stoev for the collected material and valuable discussions. The research was also supported by the Project – Nos. B-1523/05 and BG051PO001-3.3.04/41.

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A survey of spiders (Araneae) inhabiting the euedaphic soil stratum and the superficial underground compartment in Bulgaria

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doi: 10.5431/aramit4005

Abstract: In 2005 a team of Bulgarian zoologists started a project aiming to study the invertebrates inhabiting the deeper soil stratum (euedaphon) and the Superficial Underground Compartment (SUC) in Bulgaria. In the course of a four-year sampling, a total of 52 species of spiders were caught from 19 collecting sites and 9 geographical regions. They belong to the following families: Scytodidae (1), Segestriidae (1), Dysderidae (8), Nesticidae (1), Anapidae (1), Theridiidae (1), Linyphiidae (20), Agelenidae (3), Cybaeidae (1), Dictynidae (2), Amaurobiidae (2), Liocranidae (3), Corinnidae (1), Zodariidae (1), Gnaphosidae (5), and Salticidae (1). The family Anapidae, with the species *Zangherella relicta* (Kratochvíl, 1935) is recorded from three sites in the Pirin and Slavyanka mountains, and this represents the first record of the family, genus and species in Bulgaria. In spite of the active investigations of the epigean and cave spiders in these regions over the years *Z. relicta* was not found and it seems it occurs only in deeper subterranean habitats and nowhere else. Comparative study of almost topotypic specimens of *Z. relicta* from Montenegro with those collected from Bulgaria showed no variation in the shape of palp and female vulvae. Until the true identity of *Z. apuliae* (Caporiacco, 1949) from Italy is revealed, it remains unclear whether *Z. relicta* and *Z. apuliae* are conspecific, as it remains unclear whether the older records of *Z. apuliae* from the Balkan Peninsula refer to this species or to *Z. relicta*. *Pelecopsis mengei* (Simon, 1884) (Linyphiidae) and *Scotolathys simplex* Simon, 1884 (Dictynidae) are also reported from Bulgaria for the first time, the latter being also new to FYR of Macedonia. A faunistic overview of the spiders found in these underground environments is made, along with remarks on the distribution and ecology of some rare and interesting species. The presence of cave-dwelling and superficial spiders in the sampled sites indicates that SUC and euedaphon are inhabited by different ecotypes, e.g. litter- (tanathostromic), soil- (edaphic) and cave-(troglobitic) which at some places co-occur.

Key words: Anapidae, subterranean environments, troglomorphism, *Zangherella relicta*

There are various subterranean spaces that invertebrates inhabit. Depending mostly on their origins, size and distance from the surface one can distinguish different types of subterranean habitats, e.g. caves, lava tubes, microspaces in stony debris and screes, deep undreground micro- and macrospaces in the deeper gravel layers, etc. Each habitat has specific characteristics comprising temperature fluctuations, humidity, aeration, organic carbon levels, soil texture, etc. For instance daily temperature fluctuations exist in the surface of scree slopes and stony debris, while they cease completely at one-meter depth and after several dozens of metres inside large caves (RŮŽIČKA 1999). Organic carbon levels are higher in the Superficial Underground Compartment (SUC) than in caves (CULVER & PIPAN 2009). Animals that are adapted to living in complete darkness and with limited energy supplies usually acquire a specific appearance that includes depigmentation, micro- or anophthalmy, loss of wings, elaboration of extra-optic sensory structures, elongation of appendages (in cases of troglobionts) or shortening of appendages (in case of geobionts), cuticle thinning, etc. These morphological alterations known as troglomorphy are widespread in subterranean animals (CHRISTIANSEN 1962). Some species that inhabit SUC and deeper soil strata and have adapted to dwelling in these aphotic environments may have given rise to species occurring in caves (CULVER & PIPAN 2009). The vertical distribution of arthropods in the soil depends on the porosity of soil, soil type, temperature and humidity, as well as the amount of organic matter (LAŠKA et al. in press).

JUBERTIE et al. (1980) defined and described (in French) as the "Milieu Souterrain Superficiel" (MSS) one of the subterranean habitats where they found several troglomorphic invertebrates. In publications in English this particular environment is referred to as the "Superficial Underground Compartment" (SUC) or "Mesocavernous Shallow Stratum" (MSS) (Figs. 1-2). In addition to its geomorphologic structure,

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submitted: 24. 1. 2010, accepted: 6. 2. 2010; online: 10. 1. 2011

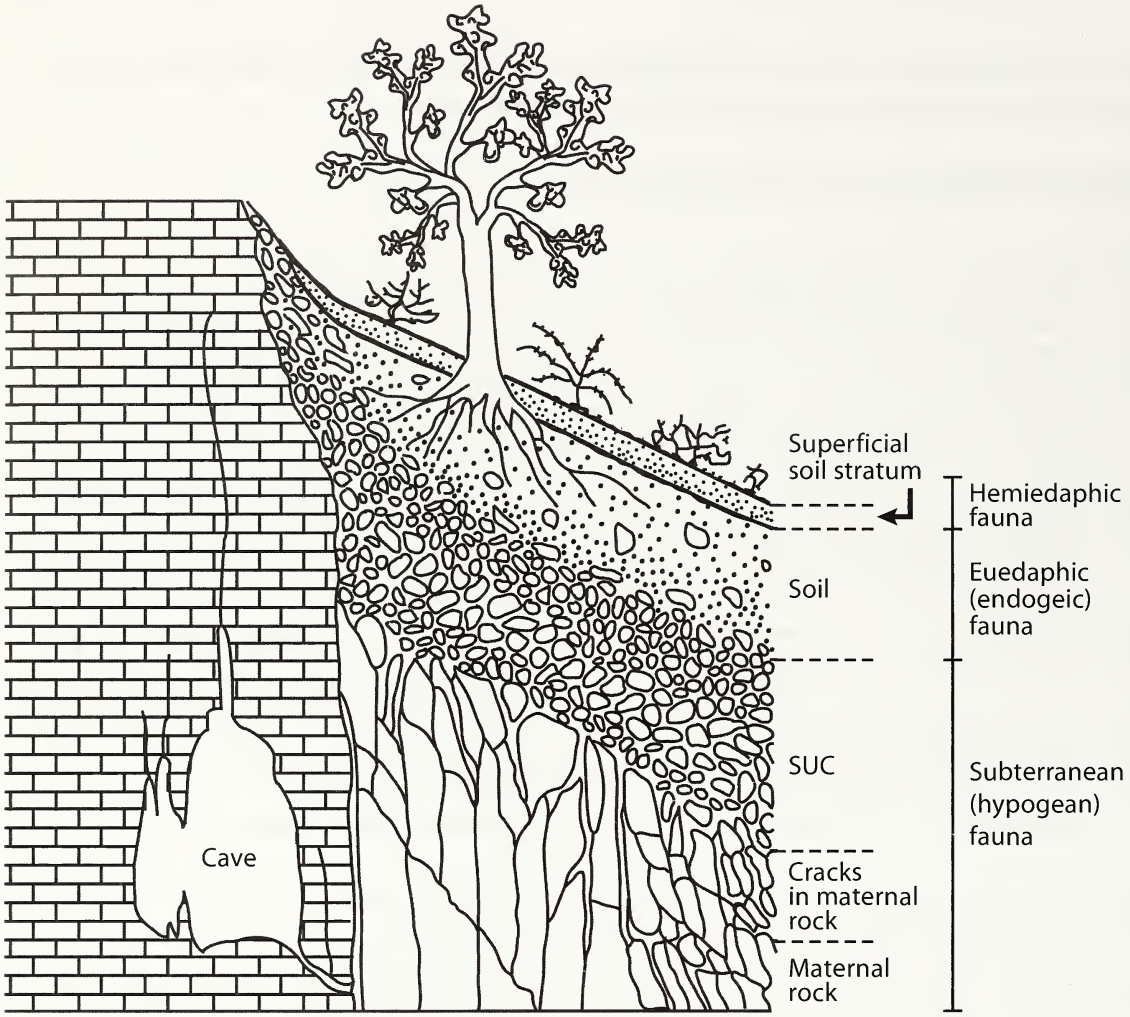


Figure 1: Structural scheme of superficial underground compartment.

the SUC has specific microclimatic and hydrological characteristics. According to JUBERTHIE & DECU (1994) the SUC exists as interconnected microspaces in valley versant screes or similar fissures in the superficial zone of maternal rocks. It connects with other profound subterranean environments like caves by way of deep fissures (NEGREA & BOITAN 2001). It is also believed that the SUC represents an intermediate stratum where litter- (tanathostromic), soil- (edaphic) and cave- (troglobitic) species may occur together. Furthermore, several SUC specialists highly adapted to subterranean manner of life inhabit the SUC and never penetrate into epigeic habitats. An example of such species is the beetle *Speonomus hygrophylus* Jeannel, 1907 (cf. CULVER & PIPAN 2009).

The euedaphic [from the Greek words "eu-" (= good) and "edaphos" (= land, earth)] soil stratum, also known as endogeic stratum is composed of mineral soil, just beneath the humus layer (cf. NEGREA & BOITAN 2001).

The most serious contribution to the study of subterranean spiders and in particular those living in the stony debris and screes in Central Europe was made by Vlastimil RŮŽIČKA, who studied the underground spider assemblages in the Czech Republic, Romania, Montenegro and Austria (see e.g., RŮŽIČKA 1989, 1992; RŮŽIČKA & THALER 2002). However, this subject received very little attention in the other parts of Europe, and yet our knowledge of the underground spider assemblages in biodiversity-rich regions such as the Balkan Peninsula remains perfunctory. A profound review of spiders living in caves and hypogeic environments can be found in RIBERA & JUBERTHIE (1994).

The spiders living in superficial, hemiedaphic and cave environments in Bulgaria have been studied

Figure 2: General view of the collecting site near Bosnek, Vitosha Mts.

quite well for almost 120 years (see e.g., DELTSHEV & BLAGOEV 2003). At the same time though very little is known about the spiders inhabiting the strata below the upper soil layer, scree slopes, stony debris, and the network of micro-crevices in the maternal rock.

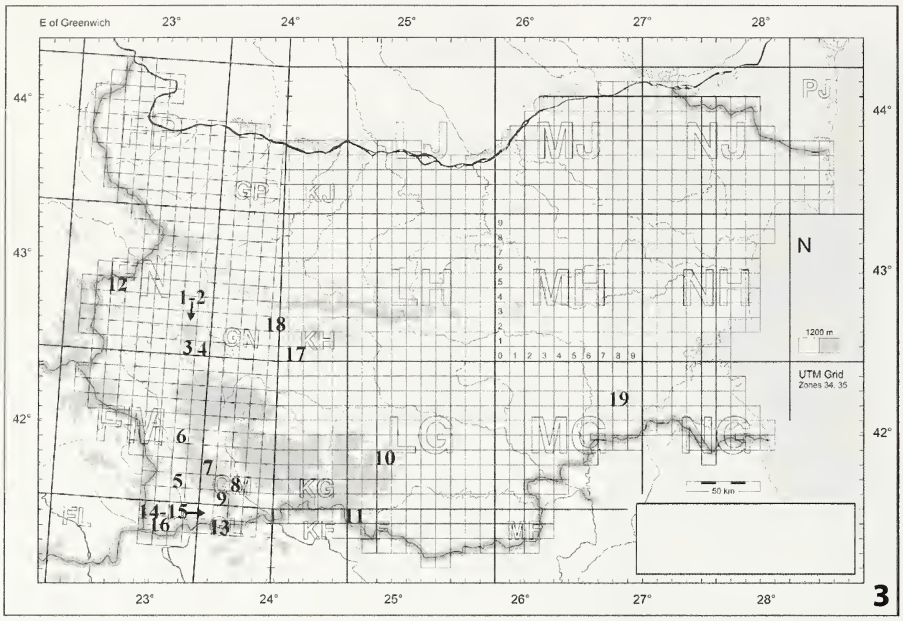
In 2005 a team of Bulgarian zoologists started a four-year project aiming to study the invertebrates inhabiting the subterranean environments in Bulgaria. Data resulting from this project have been published partially in taxonomic papers dealing with true bugs (SIMOV 2008), beetles (BEKCHIEV 2008; GUÉORGUIEV & BEKCHIEV 2009) and millipedes of the *Acanthopetalum richii* (Gray, 1832) group (STOEV 2008). Additionally, LAZAROV (2007) described the female of *Harpactea srednagora* Dimitrov & Lazarov, 1999 (Araneae: Dysderidae), a spider which was collected exclusively from subterranean habitats in Bulgaria. In other publications, LAZAROV & NAUMOVA (2010) and DELTSHEV et al. (in press), one further dysderid species was described from such environments in the Slavyanka and the Rhodopes mountains, and the thomisid spider *Cozyptila thaleri* Marusik & Kovblyuk, 2005 was reported for the first time from the country. The aim of the present study is to put on record the results of the study of the spiders inhabiting the SUC and the euedaphic soil stratum in Bulgaria.

Material and Methods

The investigation was carried out in the period April 2006 – June 2009. Forty-three traps were set in the mountains of Vitosha, Pirin, Slavyanka, Belasitsa, Ruj, Western Rhodopes, Ichtimanska and Sashtinska Sredna Gora, and the Derventsky Heights (Fig. 3, Table 1). The trap was made of a PVC pipe with a diameter of 8 cm and two different lengths: 60 and 80 cm, respectively (Fig. 4). 108 holes with a diameter of 8 mm were made in the pipe, at a distance of 10 cm from its lower end (Fig. 4) and covering nearly 1/3 of its total length. A hole of 60 to 80 cm depth was dug in the ground where the pipe was placed vertically. After the proper positioning of the pipe, the space between the pipe and the hole was filled up, initially with gravel to the upper level of the holes and subsequently with soil and other particles up to the top of the pipe. A 10-centimetre plastic pot tied to a polythene rope was put at the bottom of the pipe. The pot was filled with etylenglycol with a few drops of formalin. The trap was covered tightly with a solid plastic cover and additionally with soil, tufts of grass and leaves to prevent penetration by the superficial fauna and infiltration of water during pouring rain. Description of each collecting site and the traps is given in Table 1. Usually, traps were checked and emptied once every three months, sometimes once or twice a year. All material was sorted down to a species level and put into 70% spirit. The entire collection is preserved in the Institute of Zoology, Bulgarian Academy of Sciences (IZ). Almost topotypic material of *Zangherella relicta* (Kratochvíl, 1935) was obtained for study from the Senckenberg Museum Frankfurt (SMF). All drawings were made with a camera lucida mounted on a Wild stereoscope. Nomenclature follows PLATNICK (2010).

Results

A total of 52 species of spiders from 19 collecting sites and 9 geographical regions was collected. They belong to the following families: Scytodiidae (1), Segestriidae (1), Dysderidae (8), Nesticidae (1), Anapidae (1), Theridiidae (1), Linyphiidae (20), Agelenidae (3), Cybaeidae (1), Dictynidae (2), Amaurobidae (2), Liocranidae (3), Corinnidae (1), Zodariidae (1), Gnaphosidae (5), and Salticidae (1). The family Anapidae, with the species *Zangherella relicta* (Kratochvíl,



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Figures 3, 4: Map of the collecting sites. Numbers according to Table 1 (3); Scheme of the underground traps used in the study (4).

1935), as well as the species *Pelecopsis mengei* (Simon, 1884) (Linyphiidae) and *Scotolathys simplex* Simon, 1884 (Dictynidae) are recorded for the first time from Bulgaria (Tab. 2).

Interesting records of new or rare species

Dysderidae

Dysderids are frequent in underground habitats and in leaf-litter, and prefer warm and humid environmental conditions. Whilst there are very few cave records in Bulgaria, dysderids are quite often found in caves elsewhere and some species are even cave specialists, which have become adapted to this particular environment (e.g. CHATZAKI & ARNEDO 2006). In Bulgaria only *Harpactea babori* (Nosek, 1905) has been recorded from caves (DELTSHEV et al. 2003). Nevertheless, the family is well represented in the SUC and euedaphic stratum (Table 2), whereby species like, e.g., *Harpactea srednogora*, *H. deltshevi* and *Dysdera longirostris*, were found at several sites and were among the most abundant species in the traps. Besides depigmentation, none of the dysderids found in the underground habitats possess obvious troglomorphic features to be categorized as representing strictly geo- or troglobiontic ecomorphotypes.

Nesticidae

Nesticus cellulanus

Members of the family Nesticidae are prone to colonize shallow or deep subterranean spaces. KRATOCHVÍL (1933) described several morphological alterations in nesticids resulting from their subterranean manner of living. Out of the three species of *Nesticus* hitherto known from Bulgaria, in the SUC and euedaphic stratum we have only found *N. cellulanus*. This species is widespread throughout the country, and is among the most common spiders in Bulgarian caves (DELTSHEV et al. 2003, DELTSHEV & PETROV 2008). In the Czech Republic it occurs in shallow subterranean spaces in screes, cave entrances, and buildings (BUCHAR & RŮŽIČKA 2002).

Anapidae

Zangherella relicta (Figs. 5-13)

Pseudanapis relicta Kratochvíl, 1935: 18, pl. 1, f. 7-12. Type locality: Montenegro: 1 ♂, 1 ♀.

=?*Pseudanapis apuliae* sensu BRIGNOLI 1974, 1977, 1978, 1984, THALER & KNOFLACH 1998, nec CAPORIACCO 1949a: 4, f. 3-6.

Material examined. MONTENEGRO: 1 ♂, 1 ♀, Herceg Novi, Monastir Savina (Kotor Distr.), N42°27'7,2" E18°33'12.5", 50 m a.s.l., 11.V.2006, A. Schönhofer leg. (SMF). BULGARIA: 3 ♂♂, 2 ♀♀, Pirin Mts., village of Gospodintsi, collecting site PE, 5.V.2007, P. Stoev leg.; 2 ♂♂, Slavyanka Mts., village of Kalimantsi, collecting site S-2, 19.VI-13.VII.2007, M. Langourov and N. Simov leg. (IZ). 2 ♀♀, Slavyanka Mts., Livade, collecting site S-1, 1.VII-1.VIII.2007, N. Simov leg.

Diagnosis. Anterior median eyes absent; the palpal organ complex: cymbium and tibia fused, tegulum

Table 1: List of the collecting sites with their physical characteristics.

No	No of traps	Station	Trapping period	Geographical area	Description
1.	**1**	**VN-1**	29.IV.2006	Vitosha Mts.	Northern slope, above Boyana, Boyanski kamak place, at the bottom of a 4-5 m deep microcave; dry, alt. *ca* 850 m; N 42°38'26.8" E23°16'32.1"; UTM FN82; samples taken at 50-60 cm depth.
2.	**2**	**VN-2**	30.IV.2006	Vitosha Mts.	Northern slope, two traps set ca. 30-35 m above Boyanski kamak, scree in mixed forest of *Fagus sylvatica* and *Carpinus betulus*; alt. *ca* 850 m; N42°38'26.8" E23°16'32.1"; UTM FN82; samples taken at 40-50 cm depth.
3.	**3**	**VW**	10-24.VI.2006	Vitosha Mts.	Western slope, three traps set near the cave Duhlata, village of Bosnek, limestone, stony substrate mixed with clay, alt. *ca* 950 m; N42°29'582", E23°11'727"; UTM FN80; samples taken at 40-70 cm depth.
4.	**1**	**VE**	27.V.2006	Vitosha Mts.	Eastern slope, *ca* 28 km south of Sofia, on the road Sofia-Samokov, Yarema place; forest of *Fagus sylvatica*, in a stony, sandy substrate, humid, alt. *ca* 1400 m; UTM FN90; N42°30'289" E23°19'262"; samples taken at 60-70 cm depth.
5.	**2**	**PW**	7.V.2006	Pirin Mts.	Western slope, two traps set in the Zandana place, above village of Ilindentsi, limestone, scree, dry soil/ sandy substrate, alt. *ca* 500 m; N41°39'022" E23°15'156"; UTM FM81; samples taken at 40-60 cm depth.
6.	**1**	**PN-1**	24.V.2006	Pirin Mts.	Northern slope, *ca* 6 km before Predela, humid ravine, *Fagus sylvatica* forest, at the base of a *Fagus* tree, thick layer of leaf litter, humid soil mixed with stones, alt. *ca* 680 m; N41°55'134" E23°15'696"; UTM FM84; samples taken at 40-50 cm depth.
7.	**1**	**PN-2**	24.V.2006	Pirin Mts.	Northern slope, *ca* 150-200 m of the Baikushevata mura place on the way to hut Vihren, at the base of a scree, subalpine vegetation with scattered *Pinus mugho* trees, alt. 1900 m; N41°45'980" E23°25'233"; UTM GM03; samples taken at 40-50 cm depth.
8.	**1**	**PE**	25.V.2006	Pirin Mts.	Eastern slope, 3 km before village of Gospodintsi, Gotse Deltshev District, approx. 30 m sideward of the main road Bansko-Gotse Deltshev and *ca* 5-6 m off a small river; in a scree at the base of limestone rocks, close to a tree; alt. *ca* 600 m; N41°40'725" E23°43'502"; UTM GM21; samples taken at 40-50 cm depth.
9.	**3**	**PS**	25.V-18.VI.2006	Pirin Mts.	Southern slope, Popovi livadi Place, three traps set in a marble stone debris sideward the road and in a small valley with *Fagus* forest; alt. *ca* 1370-1560 m; N41°33 E23°37; UTM GM10; samples taken at 30-50 cm depth.
10.	**3**	**WR-1**	23.IV.2006	West Rhodopes Mts.	Central parts, three traps set *ca* 1100 m after the crossroad to village of Borovo towards the village of Belitsa; on the left side of the road, in a small rocky valley overgrown with bushes and *Pinus nigra*, *ca* 50 m sideward the road, alt. *ca* 650 m; N41°50'332" E24°51'533"; UTM LG23; samples taken at 30-70 cm depth.
11.	**1**	**WR-2**	14.VII.2007	West Rhodopes Mts.	Southern parts, near village of Koshnitsa, below the cave Uhlovitsa; right side slope, above the path, at the foot of hornbeam bushes, not far from an old *Fagus* sp. tree, humid and shady place, gravels in the soil, alt. *ca* 900 m; N41°30'802" E24°39'590"; UTM LF09; samples taken at 60-70 cm depth.
12.	**3**	**EG**	11.VI.2006	Ruj Mts.	Erma Gorge, *ca* 3 km of Tran Town, three traps set in close proximity to the tunnel; limestone, slope overgrown with hazel bush, ash-trees; rocky substrate, at the foot of rocks; alt. *ca* 700 m; N42°51'665", E22°38'949"; UTM FN34; samples taken at 40-50 cm depth.

No	No of traps	Station	Trapping period	Geographical area	Description
13.	1	S-1	4.VII.2006	Slavyanka Mts.	Livade place near the village of Goleshevo; limestone slope in a *Pinus* forest; *ca* 1700 m, N41°23'532", E23°36'307"; UTM GL18; samples taken at 40-50 cm depth.
14.	1	S-2	8.VI.2006	Slavyanka Mts.	Sveti Iliya place near the village of Kalimantsi; close to the chapel, below *Quercus coccifera* trees, alt. *ca* 500 m; N41°27'612", E23°29'448"; UTM GL09; samples taken at 40-50 cm depth.
15.	2	S-3	27.VI.2006	Slavyanka Mts.	Peshternik place, two traps set near the village of Kalimantsi; travertine, below *Salix* sp. and *Corylus* sp., alt. 380 m; N41°27'648", E23°29'680"; UTM GL09; samples taken at 40-60 cm depth.
16.	1	BE	13.VI.2008	Belasitsa Mts.	Near the village of Kamena, on the right side coast of the river Kamenitsa, *Platanus orentalis* forest, scree, *ca* 40m above the river, alt. *ca* 530 m; N41°21.460 E23°04.470; UTM FL78; samples taken at 60-70 cm depth.
17.	4	SG-1	29.IV.2006	Sashtinska Sredna Gora Mts.	Sveti Ivan place near Panagyurishte Town, four traps set in abandoned vineyard overgrown with scattered *Prunus* sp. trees and blackberries and in forest of *Pinus nigra*; deep soil layer, alt. *ca* 600 m; N42°31'004", E24°11'038"; UTM KH60; samples taken at 40-90 cm depth.
18.	2	SG-2	23.VI.2008	Ichtimanska Sredna Gora Mts.	Small church ca 2 km of village Smolsko, two traps set in front of the entrance of a small cave and in a scree close to the road, mixed broad leaved forest, alt. *ca* 600 m; N42°39'17", E23°55'11"; UTM GN42; samples taken at 40-70 cm depth.
19.	1	DH	10.V.2007	Derventsky Heights	Village of Dennitsa, close to the main motorway to the village of Stefan Karadzhovo, Yambol District, sink-hole in *Quercus* forest, at the base of a large stone; alt. *ca* 360 m; N42°15'475", E26°49'500"; UTM MG87; samples taken at 40-50 cm depth.

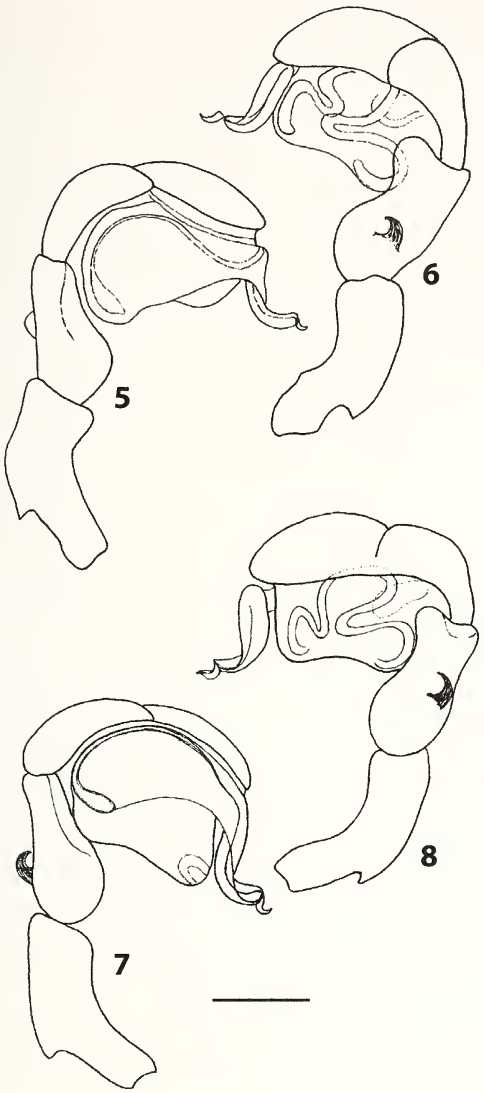
voluminous, spermophore with many coils, embolic division consisting of filiform embolus and conductor (Figs. 5-8).

Description. See e.g., KRATOCHVÍL (1935), THALER & KNOFLACH (1998).

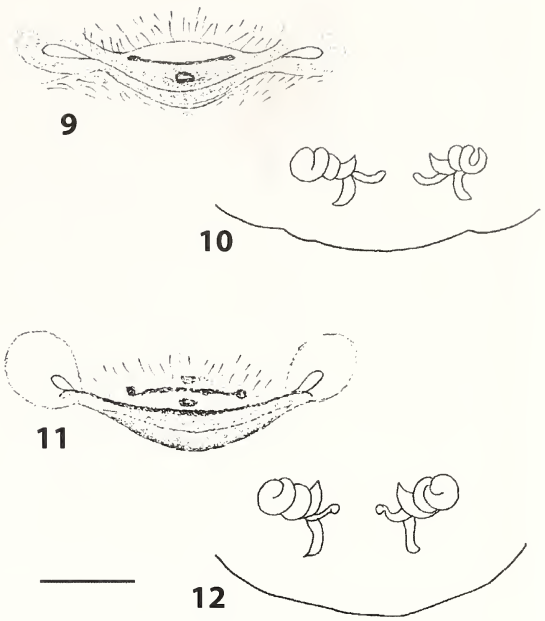
Remarks. Anapidae comprises araneoid spiders occurring in leaf-litter and moss on the ground of moist forests. The family has its highest diversity in the tropics, with only a few patchy distributed genera and species in the Holarctic region (PLATNICK & FORSTER 1989). Only two genera out of 38, namely *Comaroma* Bertkau, 1889 (1 species) and *Zangherella* Caporiacco, 1949 (3 species), occur in Europe (PLATNICK 2010).

KRATOCHVÍL (1935) described *Pseudanapis relicta* from a cave in the surroundings of Kotor, Montenegro. Later CAPORIACCO (1949a) described *Pseudanapis apuliae* from a cave in the surroundings of Otrando, Italy. The genus *Zangherella* Caporiacco, 1949 was erected by CAPORIACCO (1949b) to accommodate the species *Z. minima* from Libya. BRIGNOLI (1968) re-described *Z. apuliae* and suggested that it might be a junior synonym of *P. relicta*. In another publication (BRIGNOLI 1970) he synonymised *Z. minima* with *Pseudanapis algerica* (Simon, 1895) but later on (BRIGNOLI 1981) retracted the synonymy of the genus *Zangherella* with *Pseudanapis* Simon, 1905, and assigned to it the species *Z. algerica*, *Z. apuliae* and *Z. relicta*. Having at their disposal specimens from Greece, THALER & KNOFLACH (1998) revised the genus *Zangherella* and its distribution and stated that according to the original descriptions the main difference between *relicta* and *apuliae* concerned the number of spines on tarsus I (4 in *relicta* vs. 6 in *apuliae*). The authors studied several transitional cases where distal spines were only weakly developed and considering the completely identical shape of palps they argued that both species might actually be conspecific (THALER & KNOFLACH 1998). They also provided new illustrations of palps of specimens from Greece. The whereabouts of the type material of *P. relicta* are unknown and it is believed to have been lost during the Second World War (cf. BRIGNOLI 1968).

The almost topotypic material of *Zangherella* collected in Herceg Novi, Montenegro and the abundant material amassed using subterranean traps



Figures 5-8: *Zangherella relicta*: **5** – male palp, prolateral view; **6** – male palp, retrolateral view (Herceg Novi); **7** – male palp, prolateral view; **8** – palp, retrolateral view (Pirin Mts.). Scale bar: 0.15 mm.



Figures 9-12: *Zangherella relicta*: **9** – epigyne; **10** – vulva, dorsal (Herceg Novi); **11** – epigyne; **12** – vulva, dorsal (Pirin Mts.). Scale bar: 0.15 mm.

Figure 13: Habitus of *Zangherella relicta* (specimen from Slavyanka Mts.).

in Bulgaria made it possible to compare *vis-a-vis* the available specimens. We were not able to find any reliable differences between the Montenegrin and Bulgarian specimens when studying the structure of the vulva and the male palp (compare Figs. 5-6, 9-10 with 7-8, 11-12). They also correspond well with the illustrations of specimens of *Z. apuliae* reported by THALER & KNOFLACH (1998) from Greece. We were not able to obtain comparative material of *Z. apuliae* from Italy nor to examine the type material and could not decide whether the two species, *relicta* and *apuliae* are conspecific, as presumed by BRIGNOLI (1968). Combined molecular and morphological analysis is required to determine whether *Z. apuliae* is a valid species of a possibly restricted distribution in the Apennines or whether there is only one valid species, *Z. relicta*, distributed from the Apennines to Asia Minor.

Table 2: List of the spiders found in the euedaphic soil stratum and the SUC in Bulgaria.

Species	VN-1	VN-2	VW	VE	PW	PN-1	PN-2	PE	PS	WR-1	WR-2	EG	S-1	S-2	S-3	BE	SG-1	SG-2	DH
Scytodidae																			
Scytodes thoracica (Latreille, 1802)														X					
Segestridae																			
Segestria senoculata (Linnaeus, 1758)									X										
Dysderidae																			
Dysdera hungarica Kulczyński, 1897						X													
Dysdera longirostris Doblika, 1853			X						X				X				X	X	
Harpactea deltshevi Dimitrov & Lazarov, 1999	X	X		X						X			X						
Harpactea pr. *deltshevi*										X									
Harpactea mentor Lazarov & Naumova, 2010									X				X						
Harpactea saeva (Herman, 1879)							X					X						X	
Harpactea samuili Lazarov, 2006								X					X	X	X				
Harpactea sredgnagora Dimitrov & Lazarov, 1999		X	X			X			X	X	X	X	X			X	X	X	
Nesticidae																			
Nesticus cellulanus (Clerck, 1757)			X												X				
Anapidae																			
Zangherella relicta (Kratochvíl, 1935)								X					X	X					
Theridiidae																			
Robertus mediterraneus Eskov, 1987														X			X		
Linyphiidae																			
Antrohyphantes rhodopensis (Drensky, 1931)									X										
Centromerus acutidentatus Deltshev, 2005	X	X																	
Centromerus capucinus (Simon, 1884)																	X		
Centromerus cavernarum (L. Koch, 1872)		X										X							
Centromerus lakatnikensis (Drensky, 1931)		X	X			X	X			X			X		X		X		X
Centromerus milleri Deltshev, 1974												X							
Diplostyla concolor (Wider, 1834)			X			X		X	X	X		X	X				X		
Lepthyphantes centromeroides Kulczyński, 1914												X							
Lepthyphantes leprosus (Ohlert, 1865)	X		X		X				X		X	X							
Mansuphantes mansuetus (Thorell, 1875)							X						X						
Mioxena blanda (Simon, 1884)															X				
Palliduphantes alutacius (Simon, 1884)		X		X															
Palliduphantes istrianus (Kulczyński, 1914)	X		X								X						X		X

Species	VN-1	VN-2	VW	VE	PW	PN-1	PN-2	PE	PS	WR-1	WR-2	EG	S-1	S-2	S-3	BE	SG-1	SG-2	DH
Palliduphantes spelaeorum (Kulczyński, 1914)																X	X		
Palliduphantes trnovensis (Drensky, 1931)																		X	
Pelecopsis mengei (Simon, 1884)																	X		
Sintula retroversus (O. P.-Cambridge, 1875)													X						
Tenuiphantes tenuis (Blackwall, 1852)													X						
Walckenaeria antica (Wider, 1834)													X						
Walckenaeria mitrata (Menge, 1868)													X						
Agelenidae																			
Histopona tranteevi Deltshev, 1978										X		X	X						
Tegenaria domestica (Clerck, 1757)			X																
Malthonica silvestris (L. Koch, 1872)	X																		
Cybaeidae																			
Cybaeus balkanus Deltshev, 1997												X							
Dictynidae																			
Cicurina cicur (Fabricius, 1793)	X	X										X						X	
Scotolathys simplex Simon, 1884														X					
Amaurobiidae																			
Eurocoelotes brevispinus (Deltshev & Dimitrov, 1996)													X						
Eurocoelotes jurinitschi (Drensky, 1915)	X	X	X	X									X						
Liocranidae																			
Agroeca cuprea Menge, 1873			X																
Apostenus fuscus Westring, 1851		X																	
Sagana rutilans Thorell, 1875		X																	
Corinnidae																			
Phrurolithus festivus (C.L. Koch, 1835)			X																
Zodariidae																			
Zodarion pirini Drensky, 1921													X						
Gnaphosidae																			
Drassyllus villicus (Thorell, 1875)														X					
Echemus angustifrons (Westring, 1861)								X											
Gnaphosa modestior Kulczyński, 1897																		X	
Trachyzelotes pedestris (C.L. Koch, 1837)														X					
Zelotes erebeus (Thorell, 1871)									X										
Salticidae																			
Euophrys frontalis (Walckenaer, 1802)														X					

Distribution: *Z. relicta* is known from the cave Golobrazhnitsa and Herceg Novi, Kotor District, Montenegro (KRATOCHVÍL 1935, present study) and the mountains Pirin and Slavyanka in Bulgaria (present study). Records, possibly referable to *Z. relicta* (all sub *Z. apuliae*): Greece: Epirus (BRIGNOLI 1977, 1984), Corfu, Lefkada, Cephalonia (BRIGNOLI 1974, THALER & KNOFLACH 1998); Turkey: v. Salihli, Manisa (BRIGNOLI 1978).

Linyphiidae

Antrohyphantes rhodopensis

This species was hitherto known only from caves of the Western Rhodope Mts. and from the orophyte zone of the Rila and Pirin mountains (DELTSHEV 1996, DELTSHEV & PETROV 2008). Its presence in subterranean environments in southern Pirin adds very little to its geographical distribution but shows that the species is a subterranean specialist which is likely to be restricted to colder microhabitats and suitable humidity.

Centromerus milleri

This species was hitherto known only from Dupnitsa cave in the Strandzha Mts., the European part of Turkey (anophthalmic population, Deltshev, unpublished), Maronia cave in north-eastern Greece, several caves in the Eastern Rhodope Mts. and Stapalkata Cave in the Western Rhodope Mts., Bulgaria (DELTSHEV & PETROV 2008). The new record from the Ruj Mts. significantly extends its range in north-western direction and indicates a possibly wider distribution. The anophthalmic population in the cave Dupnitsa is of special interest, as it might represent a new, closely related troglobitic species. A molecular study of the different populations may reveal the routes of colonization, specialisation and evolution of the species in the different parts of its distribution area. The Ruj population does not show any obvious morphological difference from the other Bulgarian population.

Centromerus acutidentatus

The species belongs to the *sylvaticus*-group of the genus *Centromerus* Dahl, 1886 and is currently known from caves in Bulgaria, FYR Macedonia and Serbia (DELTSHEV & ĆURČIĆ 2002). As well as in caves, the species has also been found in the detritus of forests, and now also in the Vitosha Mts. at a depth of 40-60 cm.

Centromerus cavernarum

This species is known in Bulgaria from 10 caves in the West Rhodope Mts. (Lepenitsa, Zmiin Burun, Cheloveshkata peshtera), Stara Planina Mts. (Prelaz, Prikazna, Zlatnata peshtera), Pirin Mts. (Starshelitsa), Strandzha Mts. (Hambarcheto) and the Predbalkan (Bacho Kiro, Gurlyova dupka) (BERON 1994, DELTSHEV et al. 2003), as well as from other subterranean soil habitats. It occurs among detritus and deep under stones in beech and spruce forests, in void systems, and in screes (LASKA et al. in press). It is also quite common in caves in the Czech Republic and Slovakia (cf. RŮŽIČKA 2007).

Lepthyphantes centromeroides

This species is comparatively widespread on the Balkan Peninsula and can be considered as an example showing the process of cave colonization and subterranean adaptation. It occurs in caves, but also in the humus and ground detritus (DEELEMAN-REINHOLD 1978: 196-200).

Genus *Palliduphantes* Saaristo & Tanasevitch, 2001

The genus is represented in Bulgaria by 6 species: *Palliduphantes alutacius*, *P. istrianus*, *P. pallidus*, *P. pillichi*, *P. spelaeorum* and *P. trnovensis*. They are characteristic and widespread in caves and occur also in humus and ground detritus (DELTSHEV 1980, DELTSHEV & PETROV 2008).

Pelecopsis mengei

The species is widespread in the Holarctic region (PLATNICK 2010), and this represents the first record from Bulgaria. So far it is known only from the region of Panagyurishte, where it was found in the soil at a depth of 40-90 cm.

Agelenidae

Histopona tranteevi

So far this species was known only from a few caves in the Western Rhodope Mts. (DELTSHEV & PETROV 2008). The new records from subterranean habitats in Ruj, the Western Rhodopes and Slavyanka mountains suggest that it is much more widespread than previously thought. The species is obviously inclined to dwell in semiaphotic and aphotic environments. The Ruj locality lies quite apart from the other two and suggests that the species also occur in similar habitats in Serbia.

Dictynidae

Cicurina cicur

The majority of the species of the genus *Cicurina* (*Cicurella*) Chamberlin & Ivie, 1940 show a clear preference for life in subterranean environments, as just in North America over 60 cave-dwelling species with a different degree of cave adaptation have been described (PAQUIN & DUPÉRRÉ 2009). *C. cicur* is the only representative of this genus in Europe. As well as in subterranean habitats, it was also recorded from caves in Eastern Bulgaria (Shumen Distr. and Strandzha Mts.). It also lives under stones, in leaf-litter and in decaying wood in forests, in open habitats in microspaces with high humidity (BUCHAR & RŮŽIČKA 2002). In Germany it is active in winter (Blick pers. comm.).

Scotolathys simplex

Besides the underground samples, the species was also recently found from epigeic habitats near the village of Kamenitsa, Maleshevska Planina Mts., SW Bulgaria N 41.6496°, E 23.1607°, alt. 200 m (1♂, 1 ♀, 12.VI.2005, S. Lazarov leg.) and from FYR of Macedonia (2 ♀♀, Veles Town, near Mladost Lake, N 41.7755°, E 21.755°, alt. 240 m, 19.IV.2002, S. Lazarov leg.), which are the first records of this genus and species from both countries. The species is widely distributed in the Mediterranean region, being hitherto known from Algeria, Greece, Bulgaria, FYR of Macedonia, Spain and Ukraine (MARUSIK el al. 2009, PLATNICK 2010). GERTSCH (1946) suggested the synonymy of the genus *Scotolathys* Simon, 1884 with the genus *Lathys* Simon, 1884, but the former was recently resurrected by MARUSIK el al. (2009).

Discussion

Twenty-five per cent of the spiders (13 species) found in the SUC and euedaphic stratum are also known from caves. All of them show one or more troglomorphic traits (Table 3) and thus they could be considered true hypogeicolous animals (subterranean specialists). The remaining species are either surface dwelling (e.g. *Eurocoelotes jurinitschi*, *Gnaphosa modestior*) species or they had accidentally fallen in the traps when they were laid (*Euophrys frontalis*).

In a survey of the spiders living in deeper soil layers in the Czech Republic, LASKA et al. (in press) found 48 species of spiders, of which five, *Palliduphantes alutacius*, *Centromerus cavernarum*, *Diplostyla concolor*, *Nesticus cellulanus*, and *Cicurina cicur*, the authors considered more or less bound to subterranean environments. *P. alutacius* was found to occur at a maximum depth of 95 cm, *C. cavernarum* at 75 cm, *D. concolor* at 15 cm, and both *N. cellulanus* and *C. cicur* at 85 cm. These species were also found during our study, as *D. concolor* was found at 8 collecting sites. Another frequently collected species was *Harpactea srednagora*, which was found at 11 sites.

Of all the species found in the SUC and euedaphon only *Antrohyphantes rhodopensis*, *Centromerus milleri* and *Zangherella relicta* have a distinct troglomorphic appearance. All three are also known from caves. If we adopt the recent classification of subterranean biota (SKET 2008), where troglobionts are defined as "strongly bound to hypogean habitats", then the species mentioned above should be considered troglobionts. However, there are some alternative classifications of the subterranean animals, e.g. that of DECU et al. (2006) who distinguish between hypogeicolous and cavernicolous fauna, and further subdivide the former category into colluviotroglobitic, eluviotroglobitic, cleitrotroglobitic and volcanotroglobitic, based on the origins and texture of the substrate (colluvic, eluvic, cleitric and volcanic MSS, respectively). According to the latter classification *Zangherella relicta*, which was found only at a depth of 40-50 cm, could be considered a true colluviotroglobite, if it is proved that in Bulgaria it occurs only in the SUC and is absent in caves or superficial soil layers. *Histopona tranteevi* and *Centromerus milleri* were hitherto known only from a limited number of caves (DELTSHEV & PETROV 2008) but turned out to also live below 30 cm depth in the SUC and euedaphon. It is evident that the boundary between true troglobionts and true geobionts is very vague and there is no unequivocal tool for identifying to which of these two categories an animal belongs. Table 3 summarizes the distribution of the species found in subterranean habitats in Bulgaria and provides information on their troglomorphic traits. There are several highly adapted cavernicolous species such as *Centromerus bulgarianus* and *Troglohyphanthes drenskii*, which are so far unknown from soil strata and the SUC and might thus represent true cave-dwellers. Other troglomorphic species, which are usually considered either eutroglophiles or troglobites, such as *Centromerus cavernarum*, *C. lakatnikensis*, *C. milleri*, *Lepthyphantes centromeroides*, *Palliduphantes istrianus*, *P. spelaeorum* and *P. trnovensis* have been recorded from both caves and deeper soil strata and their habitat preferences are in need of more profound studies.

Acknowledgements

We thank Mario Langourov (IZ), Nikolay Simov (National Museum of Natural History, Sofia, NMNHS), Boyan Petrov (NMNHS), Rostislav Bekchiev (NMNHS) and Axel Schönhofer (Mainz, Germany) for providing material for this study. Vlastimil Růžička (Institute of Entomology, České Budějovice) provided valuable papers on the study of subterranean spiders in the Czech Republic and commented on the earlier version of the manuscript. We are also grateful to Mrs. Ekaterina Ivanova for providing illustrations 1 and 4. S.L. and C.D. are especially grateful to Peter Jäger and Julia Altman (SMF) for their overall support and for granting access to collections during a visit to the SMF in 2008. This paper was made possible with funding from the Bulgarian Ministry of Education and Science, The National Science Fund projects Nos. B-1523/05 and BG051PO001-3.3.04/41.

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Table 3: List of the cave-dwelling and subterranean spiders in Bulgaria with their troglomorphic traits and habitats inhabited.

Taxa	Deep Cave	Shallow cave; Cave entrances	Euedaphon and SUC	Troglomorphic traits
Leptonetidae				
Protoleptoneta bulgarica Deltshev, 1972		+		Depigmentation, elongation of legs
Protoleptoneta beroni Deltshev, 1977		+		Depigmentation, elongation of legs
Nesticidae				
Nesticus beroni Deltshev, 1977		+		Depigmentation, microphthalmy, elongation of legs
Nesticus cellulanus (Clerck, 1757)		+	+	Partial depigmentation, elongation of legs
Nesticus eremita Simon, 1879		+		Depigmentation, elongation of legs
Anapidae				
Zangherella relicta (Kratochvíl, 1935)			+	Depigmentation, microphthalmy, dwarfism
Theridiidae				
Robertus frivaldszkyi (Chyzer, 1894)	+			Depigmentation
Linyphiidae				
Antrohyphantes balcanicus (Drensky, 1931)	+			Depigmentation, microphthalmy, elongation of legs
Antrohyphantes rhodopensis (Drensky, 1931)	+	+	+	Depigmentation, microphthalmy, elongation of legs
Antrohyphantes sophianus (Drensky, 1931)	+			Depigmentation, microphthalmy, elongation of legs
Centromerus acutidentatus Deltshev, 2005		+	+	Depigmentation
Centromerus bulgarianus (Drensky, 1931)	+			Depigmentation, anophthalmy
Centromerus capucinus (Simon, 1884)		+	+	Depigmentation
Centromerus cavernarum (L. Koch, 1872)	+		+	Depigmentation
Centromerus lakatnikensis (Drensky, 1931)	+		+	Depigmentation
Centromerus milleri Deltshev, 1974	+	+	+	Depigmentation, anophthalmy, microphthalmy
Diplocephalus foraminifer (O.P.- Cambridge, 1875)	+	+		Depigmentation
Diplostyla concolor (Wider, 1834)			+	Depigmentation
Lepthyphantes centromeroides Kulczyński, 1914	+			Depigmentation, elongation of legs
Lepthyphantes leprosus (Ohlert, 1865)		+	+	Partial depigmentation, elongation of legs
Microctenonyx subitaneus (O.P.- Cambridge, 1875)	+	+		Depigmentation

Taxa	Deep Cave	Shallow cave; Cave entrances	Eudaphon and SUC	Troglomorphic traits
Palliduphantes alutacius Simon, 1884		+	+	Depigmentation, elongation of legs
Palliduphantes byzantinus (Fage, 1931)	+			Depigmentation, elongation of legs
Palliduphantes istrianus Kulczyński, 1914	+		+	Depigmentation, elongation of legs
Palliduphantes pallidus (O.P.- Cambridge, 1871)		+		Depigmentation, elongation of legs
Palliduphantes pillichi (Kulczyński, 1915)	+			Depigmentation, elongation of legs
Palliduphantes trnovensis (Drensky, 1931)	+		+	Depigmentation, elongation of legs
Palliduphantes spelaeorum (Kulczyński, 1914)	+			Depigmentation, elongation of legs
Porrhomma convexum (Westring, 1861)	+	+		Depigmentation
Porrhomma microps (Roewer, 1931)	+			Depigmentation, microphthalmy, anophthalmy
Thyreosthenius parasiticus (Westring, 1851)	+	+		Depigmentation
Troglohyphanthes drenskii Dentshev, 1973	+			Depigmentation, microphthalmy, anophthalmy
Troglohyphanthes bureschianus Deltshev, 1975		+		Depigmentation, elongation of legs
Agelenidae				
Histopona tranteevi Deltshev, 1978	+	+	+	Depigmentation, elongation of legs
Dictynidae				
Cicurina cicur (Fabricius, 1793)		+	+	Depigmentation

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The first fossil cyphophthalmid harvestman from Baltic amber

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doi: 10.5431/aramit4006

Abstract: The first fossil cyphophthalmid harvestman (Opiliones: Cyphophthalmi) from Palaeogene (Eocene) Baltic amber is described. This is only the third fossil example of this basal harvestman lineage; the others being from the probably slightly younger Bitterfeld amber and the much older, early Cretaceous, Myanmar (Burmese) amber. Although incomplete and lacking most of the appendages, the new Baltic amber fossil can be identified as a female. The somatic characters preserved, especially spiracle morphology and the coxo-genital region, allow it to be assigned with some confidence to the extant genus *Siro* Latreille, 1796 (Sironidae). This fossil is formally described here as *Siro balticus* **sp. nov.** It resembles modern North American *Siro* species more than modern European ones, and can be distinguished principally on its relatively large size and the outline form of the body.

Keywords: Cyphophthalmi, Eocene, new species, Opiliones, palaeontology, *Siro*, systematics

There are currently 29 valid species of fossil harvestmen (Arachnida: Opiliones) in the literature; see DUNLOP (2007) for an older summary. Since 2007 a further species belonging to Cyphophthalmi has been described from early Cretaceous (ca. 100 Ma) Myanmar (Burmese) amber (POINAR 2008). Long-legged and rather modern-looking Eupnoi material, partially assignable to the extant family Sclerosomatidae, is now known from the mid Jurassic (ca. 160–180 Ma) of Daohugou, Inner Mongolia, China (HUANG et al. 2009). Both records are highly significant given the relative rarity of both Asian fossil arachnids and Mesozoic Arachnida in general. DUNLOP & MITOV (2009) described further specimens belonging to Eupnoi and Dyspnoi in the German Bitterfeld amber; the age of which is controversial, but which may be Oligocene (ca. 24–25 Ma). Some of these records are of species previously recorded from the older (Eocene, ca. 45–50 Ma) Baltic amber. Two further Bitterfeld species were described as new, and one is effectively indistinguishable from, and potentially conspecific with, a living Caucasus harvestman species.

Cyphophthalmids (mite harvestmen) are widely recognised as the most basal lineage of Opiliones (e.g. GIRIBET et al. 2002, 2010: Figs. 9–10) and yet they show the poorest fossil record of any of the major harvestman groups. This may well be a consequence of the small size and cryptic lifestyle of these superficially mite-like animals, which significantly reduces their potential for fossilisation. While conceding the inherent imprecision in age estimates, the phylogeny of

Figures 1-2: *Siro balticus* sp. nov.; holotype (F2147/BB/CJW). The first record of a fossil mite harvestman (Arachnida: Opiliones: Cyphophthalmi) from Eocene (ca. 45–50 Ma) Baltic amber. – **1**: Dorsal view. – **2**: Ventral view. Scale bar equals 1.0 mm.

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submitted: 10.12.2009, accepted: 26.4.2010; online: 10.1.2011

GIRIBET et al. (2010) predicted a possible diversification age (as opposed to origins) for Cyphophthalmi of ca. 345 Ma (i.e. early Carboniferous). This postdates the oldest known harvestman (probably an eupnoid) which is early Devonian (ca. 410 Ma) in age.

The extant cyphophthalmid fauna currently comprises 168 species (MURIENNE et al. 2010). The first fossil example of a cyphophthalmid, *Siro platypedipus* Dunlop & Giribet, 2003, was described from Bitterfeld amber and assigned to the extant genus *Siro* Latreille, 1796 (Sironidae). A second species, *Palaeosiro burmanicum* Poinar, 2008 was described from Cretaceous Myanmar amber (see above). It was assigned to a new (extinct) genus, also in the family Sironidae, based on the combination of its small size, the presence of type 2 ozophores, round spiracles, and a large sternal gland on the first sternite (POINAR 2008). In terms of biogeography (e.g. BOYER et al. 2007, Fig. 1) its assignment to Sironidae is probably incorrect (Giribet pers. comm.), given that only the family Stylocellidae occurs in this region of SE Asia today. Based on the putative presence of a cuticular lens and microvilli in the ozophores Poinar suggested that these structures may also have functioned as light-sensitive organs, in addition to their function in releasing defensive secretions. A more prosaic interpretation would be that that the translucent areas at the ends of the ozophores merely reflect fluid released during the entrapment process.

Here, we report on only the third fossil example of a cyphophthalmid (Figs. 1–3, 5–6). The specimen is incomplete which makes detailed comparisons with other extant and fossil taxa (cf. KARAMAN 2009 and references therein) difficult. However some genus-specific characters can indeed be recovered and we can provisionally assign it to a new species of *Siro*; representing the first record of the genus from Baltic amber.

Material and Methods

The new fossil described here is from the Jörg Wunderlich collection, specimen number F2147/BB/CJW. This material will probably be transferred eventually to the Senckenberg Museum, Frankfurt/Main, Germany, or one of its allied institutions. The specimen lies in a subrectangular block of clear, yellow amber; dimensions ca. 25 × 15 mm. It was extracted from a larger amber piece (number F2159) in order to reveal the ventral surface of the harvestman more clearly.

The fossil was photographed (Figs. 1–2) by taking sequential series of ca. 10 images at different focal planes through the specimen using a Leica stereomicroscope with the Leica Application Suite software. Stacks of images were assembled into a single final picture using Auto Montage. It was drawn and studied under a stereomicroscope with a *camera lucida* attachment (Fig. 5–6). The fossil was compared to extant cyphophthalmids in the collections of the Museum für Naturkunde Berlin and the personal collection of P.G. Mitov, as well as to the literature; particularly JUBERTHIE (1970), GIRIBET & BOYER (2002) and KARAMAN (2009), from whom the morphological terminology used is largely adopted. Terms for the description of the coxo-genital region are based on HOFFMAN (1963) and VAN DER HAMMEN (1985).

Further data on the distribution of modern genera was retrieved from the catalogue of GIRIBET (2000), now updated online and including numerous images of extant taxa under <http://giribet.oeb.harvard.edu/Cyphophthalmi/>. An exact provenance for the new fossil specimen is not recorded, but much of the currently available amber derives from the Kaliningrad region on the Baltic coast of Russia. An exact age for amber is difficult to determine objectively, but Baltic amber is traditionally dated at Paleogene (Eocene), or about 45–50 Ma.

For comparative purposes, a scanning electron micrograph (SEM) photograph of the genital region of a recent cyphophthalmid harvestman is also included here (Fig. 4): 1 female *Cyphophthalmus duricorius* Joseph, 1868: Slovenia, 4 km NW from Postojna, Pivka Jama camp site, under stones in the old pine forest (N 45°48'18.28" E 14°12'16.01", 550-579 m a.s.l.), 16.IX.1989, leg. and det. P. G. MITOV. The SEM study was made at 10–20 kV with a Philips 515 machine. The specimen was sputter-coated with a 300–400 Å gold layer. Further SEMs of the American species *Siro exilis* Hoffman, 1963 were kindly provided by Günther Raspotnik (Figs. 7–8): 1 female *Siro exilis* Hoffman, 1963: West Virginia, Randolph Co., Monongahela National Forest, nr. Bowden; Otter Creek Wilderness trailhead near Alpena Gap, deep litter of mixed riparian forest (red maple, yellow birch, eastern hemlock, white spruce) with dense understory of rhododendron, 930 m a.s.l., 38° 56.505' N, 79° 40.084' W, 13.VI.2006, leg. and det. Roy A. Norton.

The specimen was air-dried, mounted on an aluminium stub and sputtered with gold (AGAR sputtercoater, Gröpl, Tulln, Austria). The SEM study was made at 20 kV with a Philips XL30 ESEM (Philips/

FEI, Vienna, Austria) at high vacuum mode.

Order Opiliones Sundevall, 1833
Suborder Cyphophthalmi Simon, 1879
Family Sironidae Simon, 1879
Genus *Siro* Latreille, 1796
***Siro balticus* sp. nov.**

Material: Holotype ♀ and only known specimen, JÖRG Wunderlich collection, F2147/BB/CJW. From Baltic amber, exact locality not recorded; Paleogene, Eocene.

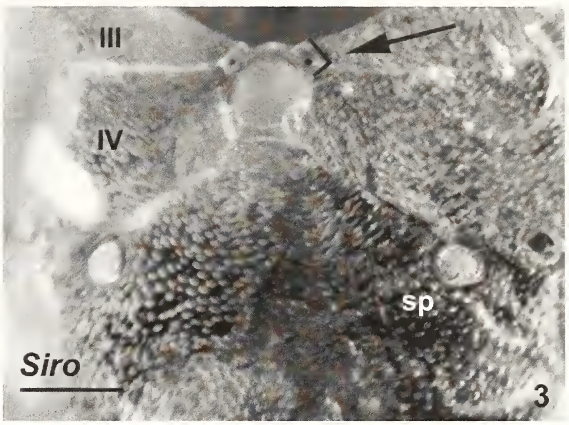
Diagnosis: Relatively large (length 2.34 mm) fossil *Siro* species, specifically without the projecting rear end typical of modern European forms, and with body proportions differing from those in the – probably more closely related – extant North American species (see Remarks for details).

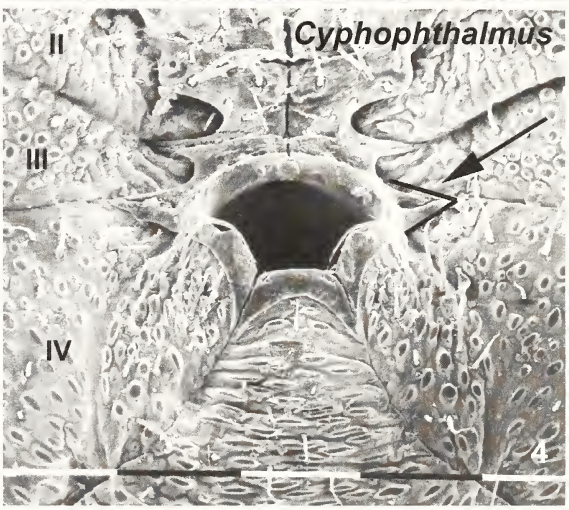
Derivation of name: From Baltic amber and the Baltic region; the source of this material.

Description: Partially complete female specimen preserved in both dorsal (Figs. 1, 5) and ventral view (Figs. 2, 6). All measurements in mm. Body oval; pale brown in colour within the amber, but with darker patches across the body; total length 2.34; maximum prosomal width behind the ozophores 1.33; maximum opisthosomal width 1.34. Length:width ratio 1.75. Distance between front of scutum (i.e. anterior margin of prosoma) to an imaginary line connecting the anterior (front) bases of ozophores 0.23; total width across (and including) ozophores 1.09.

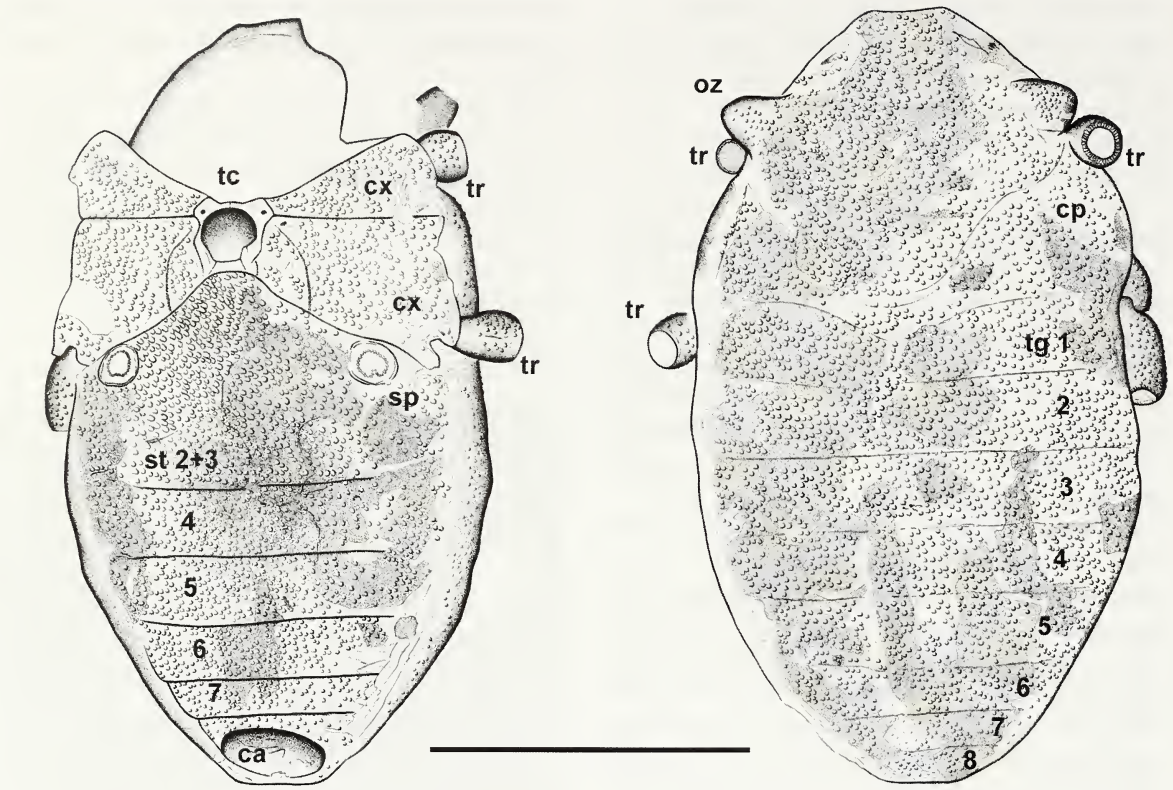
Entire body with pustulate ornament of small, rounded to oval tubercles, generally larger in anterior body regions and smaller posteriorly and on the leg trochanters. Eyes absent. Ozophores conical to slightly pointed and angular, dorsolaterally prominent on the scutum in the type 2 position sensu JUBERTHIE (1970, Fig. 2). Exact position of the ozopore itself – i.e. the opening of the repugnatorial gland – difficult to resolve, but may be terminal. Length of ozophores 0.13; width at base 0.22. Slight bulge to body immediately behind the ozophores. Frontal ridge of scutum (i.e. anterior margin of carapace) slightly recurved. Sulcus beginning immediately behind the ozophores curves down towards the midline and defines a posteriorly deeply recurved anterior area of the body; length 0.84 on the midline. Area behind it incorporates the bulge in the body laterally and is also recurved at the midline, length here 0.12. This region followed by eight, quite clearly defined, tergites all with essentially straight posterior margins. Gaps between tergites lack tuberculation. Anterior four tergites longer, lengths c. 0.2; posterior three are notably shorter, lengths 0.13, 0.11 and 0.12 respectively. Posterior end of opisthosoma bluntly rounded to slightly angular in dorsal view.

Ventral prosomal complex incomplete. Chelicerae, pedipalps, coxae of legs 1–2 and all walking legs beyond the trochanter absent. Conceivably, the missing coxae (I–II, or perhaps II only) were free, i.e. not fused to coxae III–IV; which could explain why the breakage point in the fossil lies between the second and third coxae. Third coxae triangular, coming to a point immediately above the thoracic complex, but not quite reaching the midline. Third trochanter somewhat





Figures 3-4: Details of the thoracic complex region. – **3**: *Siro balticus* sp. nov.; holotype (F2147/BB/CJW). The rounded spiracle (sp) with denticles inside the lumen is a convincing character of the genus *Siro* Latreille, 1796. Coxae numbered. The area between coxal lobes III and IV (i.e. around the coxal pores) has an obtuse, ca. 90°, angle (outlined by black bars: arrowed); another *Siro* character. Scale bar equals 200 µm. – **4**: Same region in a modern cyphophthalmid, *Cyphophthalmus duricorius* Joseph, 1868, SEM. Scale bars equal 100 µm. In *Cyphophthalmus*, by contrast, the area between coxal lobes III and IV has a very acute angle (outlined by black bars: arrowed).



Figures 5-6: Interpretative *camera lucida* drawings of the specimen shown in Figs. 1–2. **5**: Dorsal view. – **6**: Ventral view. Abbreviations: ca = expected site of corona analis, cp = carapace, cx = coxa, oz = ozophore, sp = spiracle, st = sternites 2+3 (subsequent sternites numbered successively), tc = thoracic complex, tg1 = tergite 1 (subsequent tergites numbered successively), tr = trochanter. Scale bar equals 1.0 mm.

rounded and cup-shaped, but details equivocal. Fourth coxae much larger than the third and more quadratic in shape. Distinct suture line originates near the anterolateral corners of the thoracic complex and curves towards the posterior margin of the coxae, bisecting it about a third of the way along its length towards the distal margin. Fourth trochanter emerges from the posterior part of the fourth coxae and is associated with a small, but distinct indent into the coxal margin. Trochanter 4 tubular, longer than wide and with a slightly oval outline, widening distally, length 0.28.

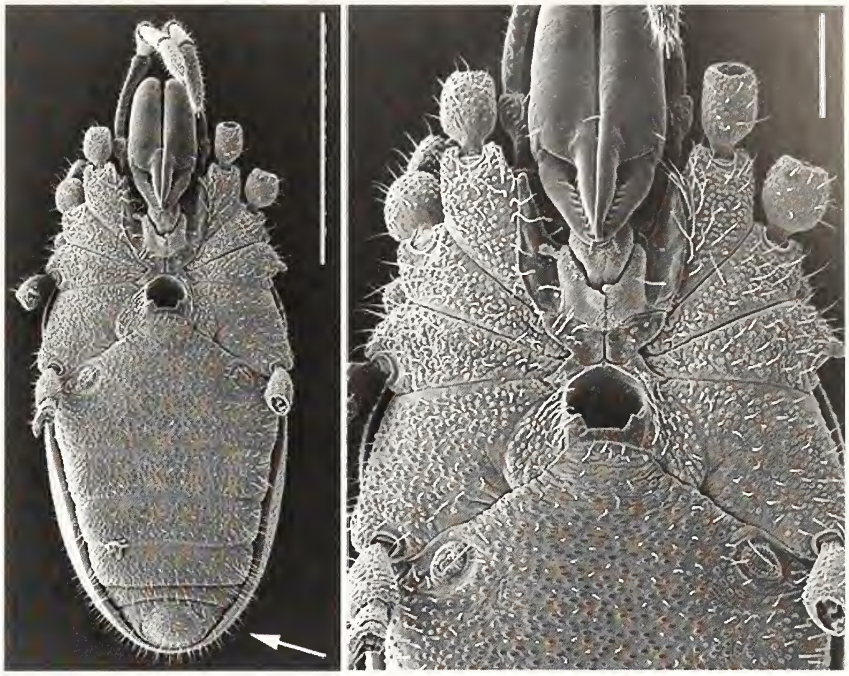
Thoracic complex with the outline of an inverted subtriangular structure, dominated centrally by large genital opening (or gonostome) of the female type (Fig. 3). Gonostome anteriorly with semicircular outline; width 0.17, length 0.16; no genital structures visible within this opening. Thoracic complex flanked laterally by sutured-off part of the fourth coxae, posteriorly by the second sternite and anteriorly (in part) by the third coxae. More anterior elements missing. Thoracic complex divided anteriorly by a short midline sulcus. Either side of this, i.e. on the anterolateral margins of the gonostome, are areas surrounding the coxal pores (= orifices of the coxal glands). Pores themselves clearly visible as small, but distinct holes, diameter 0.0125, lying between coxal lobes III and IV.

Sternites two and three apparently fused into a single, large subtriangular plate, projecting anteriorly between the leg 4 coxae with a procurved and bluntly rounded anterior margin pointing towards the thoracic complex. Tuberculation here heavier, with larger and more oval tubercles. Spiracles present as prominent, round to oval-shaped elements (maximum diameter 0.16) in a lateral position immediately behind the fourth coxae; ring of tiny denticles present within the lumen, expressing – at least on the right side – a distinct invagination towards the centre of the spiracle. No obvious sternal pores, or other structures, located on the midline between the spiracles.

Five sternal elements (presumably sternites 4–8) preserved behind the large, spiracle-bearing sclerite. Sternites 4–7 decrease successively in length: i.e.

0.20, 0.19, 0.16 and 0.10. Sternite 8 forms the anterior border of a fairly large oval opening, width 0.32, which in life would probably have contained the corona analis. Posterior margin of opisthosoma somewhat blunt and rectangular in ventral view; i.e. not smoothly rounded, but details of any specific sclerites here difficult to resolve. In general, tergites slightly wider than sternites and marginal overlap from the overlying tergites can be seen ventrally at the lateral edges of the body.

In cyphophthalmids the form of the gonostome differs between the sexes and this specimen clearly has the female type. Since the gonostome is preserved open (Fig. 3), it must be an adult and is thus clearly a mortality rather than a moult.



Figures 7-8: Comparative SEM images of a female of the Recent species *Siro exilis* Hoffman, 1963 from the eastern USA. These eastern *Siro* species are thought to be closer to the European fauna than those of the western USA (cf. Shear 1980). **7**: Overview. Scale bar equals 1.0 mm. Note the overall similarity to the fossil *Siro* species in terms of the absence of a projecting rear end (arrowed); a feature usually seen in the (modern) European forms. – **8**: Detail of spiracles and thoracic complex region. Scale bar equals 200 µm.

Intuitively, the new fossil with its distribution in the Eocene of northern Europe is likely to be a member of Sironidae (see e.g. GIRIBET (2000: Fig. 2) or BOYER et al. (2007: Fig. 1) for distribution maps) because none of the other extant cyphophthalmid families occur in this region today. The fossil is unquestionably modern in appearance and affinities with a number of extant genera need to be considered: i.e. *Siro* Latreille, 1796, *Cyphophthalmus* Joseph, 1868 (re-established by BOYER et al. 2005 for a Balkan radiation; see also KARAMAN 2009 and MURIENNE et al. 2010) and the four Iberian genera most recently investigated by MURIENNE & GIRIBET (2009). These taxa are morphologically rather conservative and appear similar in overall habitus, while a number of taxonomically important details are missing from the new fossil which hinders its unequivocal generic assignment.

KARAMAN (2009: table 1) established a series of characters useful in separating *Siro* from *Cyphophthalmus*. Some of these, such as the number of paired, movable fingers associated with the spermatopositor, the number of anal glands, and the shape of the adenostyle of the tarsal gland apophyses, only occur in males and are thus unhelpful in placing this female fossil. An alternative character (cf. KARAMAN 2009: p. 262) which would have been useful is the shape and structure of the prosomal complex (i.e. the coxal lobes of legs II, immediately in front of the genital opening), but unfortunately this feature is equivocal in the fossil.

A character discussed by KARAMAN (2009) which is preserved is the form of the spiracles and this does offers useful data about the animal's affinities. In *Cyphophthalmus* the spiracles are semicircular, each with a conical cuticular projection on its posterior margin. This is not seen in the fossil, which by contrast (Fig. 3) seems to share a character seen, so far, only in *Siro* and which consists of a more rounded spiracle (of circular type, sensu GIRIBET & BOYER 2002), with denticles inside the lumen (cf. BIVORT & GIRIBET 2004: Fig. 36c, KARAMAN 2009: Figs. 2A–B). For this reason we are confident in our generic assignment of this fossil to *Siro*. In support of this hypothesis we also note that the form and width of the area between coxal lobes III and IV is very different between *Siro* and *Cyphophthalmus* species. Specifically, the endites (= coxapophysis) of coxae III and IV form either an area (around the coxal pores) with a very acute angle

(in *Cyphophthalmus*: Fig. 4) or a right/obtuse angle (in *Siro*: Fig. 3); thus in this context the amber fossil more closely resembles female *Siro* species. For comparative figures of *Siro* see e.g. RAFALSKI (1958: Fig. 7) for *Siro carpaticus* Rafalski, 1956, JUBERTHIE (1967: Fig. 7) for *Siro rubens* Latreille, 1804, and NOVAK & GIRIBET (2006: Figs. 5, 7, 12) for *Siro crassus* Novak & Giribet, 2006. For various *Cyphophthalmus* species we refer also to EISENBEIS & WICHARD (1987: Plate 27, d) (sub *Siro duricorius*), MITOV (1994, Fig. 23) (sub *Siro beschkovi*) or KARAMAN (2008, 2009).

Although incomplete, we feel able to assign this new fossil to its own species. Of particular interest is the posterior end of the body. Females of modern European *Siro* species typically show a projecting rear end (see e.g. figures in JUBERTHIE 1970), whereas the Baltic amber example has a more smoothly rounded back end which thus resembles, the North American *Siro* species (e.g. NEWELL 1943, 1947, HOFFMAN 1963, SHEAR 1980; see also Fig. 7). Conceivably our fossil was part of this (formally Laurasian?) lineage (see Discussion). At 2.34 mm in body length the new fossil sironid is somewhat larger than typical American *Siro* species. Body lengths of females vary from 1.10 mm (in *Siro sonoma* Shear, 1980) to 2.08 mm (in *Siro exilis* Hoffman, 1963 – the largest modern American sironid); see also NEWELL (1943, 1947). The largest European sironid is the epigean *Siro crassus* Novak & Giribet, 2006 in which females reach 2.40-2.61 mm.

Direct comparison with the previously described European amber species, *Siro platypedibus*, is difficult given that the fossils are preserved in completely different orientations. The coxo-genital and anal region of the younger Bitterfeld fossil cannot be resolved. The originally proposed diagnosis was based on its flattened legs; a character which cannot be tested in the Baltic form. In any case this has recently been challenged as a possible artefact by KARAMAN (2009). He noted that limb flattening can occur while making preparations of extant material in various mounting media, and that the amber-forming resin as a similarly concentrated viscose medium could have induced comparable effects. Our new fossil and *S. platypedibus* are, at ca. 2 mm long, similar in overall size. While it may be possible to draw some comparisons based on the profile of the body sculpture in these respective fossils, we currently have little data to argue either for or against the conspecificity of these extinct taxa from the different amber faunas.

Discussion

As noted above, GIRIBET et al. (2010) inferred a basal divergence time for modern cyphophthalmid lineages perhaps as far back as the Carboniferous (ca. 345 Ma); at which time Europe and North America were part of the single palaeocontinent Laurasia. Indeed, SHEAR (1980, p. 4) commented on the strong similarities between some of the (eastern) N. American cyphophthalmids and the European fauna: "... the original divergence took place between the western species and *S[iro] exilis* (Figs. 7–8) plus the European forms. The movement of North America away from Europe and Africa, which resulted in the opening of the present Atlantic Ocean, may account for the separation of *S. exilis* from its European relatives." The hypothesis that the North American *Siro* species are not monophyletic was again supported in a recent study by GIRIBET & SHEAR (2010), who further recovered European affinities for some American taxa under some parameters of analysis and reiterated the idea that *Siro* may be a very ancient genus.

What this implies is, first, that there is no fundamental objection to recovering an American-like *Siro* species from Baltic amber. This lineage may well have been originally distributed more widely across the Palaearctic, and was present in north-central Europe during the presumably warmer conditions associated with the Baltic amber forest. A possible parallel example of this would be the eupnoid harvestman genus *Caddo* Banks, 1892 which was also present in Europe during the early to mid-Paleogene (DUNLOP & MITOV 2009, and references therein), but is absent from the modern European fauna and yet still found today in North America. Second, the opening of the Atlantic began during in the Triassic (ca. 200–250 Ma), and this, in turn, offers a minimum divergence time, based on geological evidence, for a common ancestor of these similar-looking American and European *Siro* species; the latter also including *Siro balticus*.

To reiterate, North America yields *Siro* (cf. GIRIBET & SHEAR 2010), while both *Siro* and *Cyphophthalmus* occur in Europe. In recent studies *Cyphophthalmus* was treated as a specifically Balkan radiation (BOYER et al. 2005, KARAMAN 2009); although we should note that *Siro* has also been reported at least as far south as Slovenia (NOVAK & GIRIBET 2006). Recent work by MURIENNE et al. (2010) inferred a late Cretaceous radiation for *Cyphophthalmus* of ca.

94 Ma and attempted to tie the explosive evolution of its numerous endemic species into the wider geological development of the Balkan Peninsula. Slow rates of evolution for cyphopthalmids in general were postulated by SHEAR (1980) – see also GIRIBET & SHEAR (2010) – and the modern appearance of this amber fossil (cf. Figs. 1-2 and 7-8) compared to extant forms tends to support this supposition: at least for *Siro*. Unfortunately, we still lack Palaeozoic cyphophthalmids which should date from the early phase of their evolution as predicted by molecular analyses.

Acknowledgments

We thank Jörg Wunderlich (Hirschberg) for making this material available for study and preparing the specimen from a larger block of resin, as well as Ivo Karaman (Novi Sad) and Gonzalo Giribet (Harvard) for valuable comments and to Gonzalo for providing pre-publication copies of relevant papers. Günter Raspotnik (Graz) kindly provided SEM images of *Siro exilis* material, which in turn was made available by Dr. Roy Norton (SUNY-ESF, Syracuse, New York). Finally, the reviewers are also thanked for helpful remarks.

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Spiders in a hostile world (Arachnoidea, Araneae)

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doi: 10.5431/aramit4007

Abstract: Spiders are powerful predators, but the threats confronting them are numerous. A survey is presented of the many different arthropods which waylay spiders in various ways. Some food-specialists among spiders feed exclusively on spiders. Kleptoparasites are found among spiders as well as among Mecoptera, Diptera, Lepidoptera, and Heteroptera. Predators are found within spiders' own population (cannibalism), among other spider species (araneophagy), and among different species of Heteroptera, Odonata, and Hymenoptera. Parasitoids are found in the orders Hymenoptera and Diptera. The largest insect order, Coleoptera, comprises a few species among the Carabidae which feed on spiders, but beetles are not represented among the kleptoparasites or parasitoids.

Key words: aggressive mimicry, araneophagy, cannibalism, kleptoparasitism, parasitoid

Spiders are successful predators with important tools for prey capture, viz, venom, diverse types of silk for snaring and wrapping, and speed. But spiders are prey for other organisms as well. This paper presents a survey of all the threats spiders have to face from other arthropods (excluding mites), based on data from the literature and my own observations. Spiders are often defenceless against the attacks of others, just as most spider victims are defenceless against the spiders and their methods of capturing prey. In this article I look at the spider in its environmental context from four angles: when it is preyed on by other spiders; when it is the victim of kleptoparasites (spiders and insects) which steal food from its web; when it is preyed on by other invertebrates (other than spiders); and when the individual spider falls victim to parasitoids. The subjects are dealt with in this order (Fig. 1). The present study is restricted to arthropods.

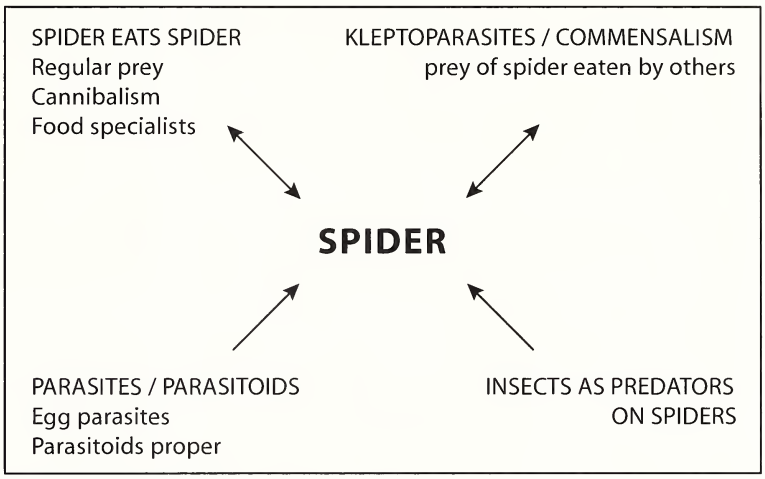

Figure 1: The spider in its environmental web.

Many of the relationships referred in this article come from subtropical and tropical regions where biodiversity is much higher and food specialization apparently has a better chance to develop. Nevertheless, the temperate regions contribute to the ecological interactions dealt with here, too.

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submitted: 27.11.2009, accepted: 27.4.2010; online: 10.1.2011

Spiders and their prey

The regular prey of spiders consists of insects and other invertebrates, including other spiders. The methods employed are hunting, by sight or other senses, or catching with a web which has sticky threads or is made to entangle the prey. Prey can be wrapped up in silk or held with the legs and chelicerae but as a rule are killed with venom and digested externally by regurgitating digestive fluid over the prey after which the resulting fluid is sucked up. Walking, stalking, waiting, and wrapping are terms which fit. Although the bulk of spider prey consists of insects, preying on spiders is not an exception.

A general phenomenon in spiders is cannibalism which can already take place inside the egg batch or within the population. SAMU et al. (1999) demonstrated, for *Pardosa agrestis* (Westring), that when food is scarce preying on individuals in the

same population becomes common. Usually not all specimens in a population are of the same age and size as they come from different egg batches and larger individuals then tend to eat the smaller members of the population. Some spiders have distinct food preferences. It is common knowledge that *Dysdera* species specialize on woodlice (Isopoda), bolas spiders (Araneidae: *Mastophora*, *Ordgarius*) attract male moths with chemical compounds which resemble the moth's pheromones, while *Zodarion* species feed on ants. Mimetidae and some Salticidae feed exclusively on other spiders, while some Pholcidae hunt other spiders as well (see section "Insects and spiders as predators on spiders").

Kleptoparasites

Kleptoparasitism is found in spiders as well as in many insect orders. Prey in spider webs are apparently an easily obtainable source of food once one has developed a method of getting at it without alarming the owner of the web and becoming its prey. Examples are summed up by order.

Araneae

Kleptoparasites "steal" the prey of the spider from the spider's web. It is debatable if this might be called commensalism, which is defined as using the food of the host species without causing any harm or negative influence. In many instances, e.g. with web-building species, a spider obtains food by locating the prey in the web, biting it and injecting venom, regurgitating digestive fluid over the prey, and wrapping the victim. All these actions are energy investments made by the host spider and thus are of negative influence on its energy balance, however slight. A kleptoparasite profits from the host spider's energy investment without giving anything in return. True kleptoparasites are able to walk along sticky silk without being trapped. This is not so surprising for kleptoparasitic spiders in which the ability to walk on webs is common in many groups. For other invertebrates this quality must have evolved.

Kleptoparasitism occurs in a large number of spider families (Anapidae, Dictynidae, Eresidae, Mysmenidae, Oonopidae, Salticidae, Sparassidae, Symphytognathidae, Theridiidae, and Uloboridae) (for a summary and literature references, see AGNARSSON 2002). *Argyrodes* species (Theridiidae) are the best-known examples of kleptoparasitism and are found with orb web building Araneidae and Tetragnathidae, and social and subsocial spiders with large communal webs, such as *Anelosimus* (AGNARSSON 2003). *Argyrodes* steals the prey and may carry it off to the margin of the web (AGNARSSON 2003). Larger webs, such as those of *Nephila*, often catch more small prey than the owner needs. Small prey specimens just stick to the spiral threads and are not even bitten or wrapped and *Argyrodes* often eats from such neglected prey. The habit runs through the whole genus. *Argyrodes bryantae* Exline & Levi was found as kleptoparasite in the webs of *Tengella radiata* (Kulczynski) (EBERHARD et al. 1993). *Argyrodes antipodianus* O.P.-Cambridge shows a transition to araneophagy (WHITEHOUSE 1986). Social Uloboridae have been observed as solitary kleptoparasites in the webs of other spiders. *Philoponella republicana* (Simon) is known to occur in webs of *Cyrtophora nympha* Simon (ROBINSON 1977) and also in *Anelosimus* webs in French Guiana (LOPEZ 1987). *P. tingena* (Chamberlin & Ivie) has been recorded from webs of *Nephila clavipes* L. and "*Achaearanea* spec." (OPELL 1979). Two species of *Mysmenopsis* (Mysmenidae) lead a kleptoparasitic life in webs of *Tengella radiata* (Kulczynski) (Tengellidae) (EBERHARD et al. 1993). Both have a broad host spectrum. *M. tegellacompta* Platnick is found in webs of *Tengella radiata* as well as in a diplurid web and an agelenid web (species not established), while *M. dipluramigo* Platnick & Shadab has been found in webs of *T. radiata*, a ctenid web and a pisaurid web (EBERHARD et al. 1993).

Mecoptera

Scorpionflies (Mecoptera) of the family Panorpidae have been observed to land directly onto a spider web or walk into it from the surrounding vegetation and eat from the prey they find there. When the owner of the web approaches the scorpion fly it may ward the spider off by hitting it with the thick end of its abdomen. Scorpionflies have been found in webs of Agelenidae, Tetragnathidae, Theridiidae, and Araneidae (THORNHILL 1975).

Diptera

Diptera also have their kleptoparasitic species. The gall midge *Didactylomyia longimana* (Nematocera, Cecidomyiidae) was detected as a very common kleptoparasite in orb webs of *Nephila clavipes* (Tetragnathidae), *Argiope aurantia* Lucas, *Mastophora bisaccata* (Emerton), *Eriophora ravilla* (C.L. Koch), and *Scoloderus cordatus* (Taczanowski) (all Araneidae) (SIVINSKI & STOWE 1980). The females were found on the prey of the spider, while the males were hanging inactively in the web. Among the biting midges

(Ceratopogonidae) a number of species associated with spider webs have also been found (SIVINSKI & STOWE 1980).

Among the suborder Brachycera there are several families which comprise species with kleptoparasitic behaviour. Examples of species of Chloropidae and Milichiidae (both of acalyptrate fly families) are listed by NENTWIG (1985). *Desmometopa* species (Milichiidae) were observed to feed on the prey (honey bee, *Apis mellifera*) of a lynx spider (Oxyopidae, probably *Oxyopes heterophthalmus* (Latreille)) and also of other spiders (RICHARDS 1953; ROBINSON & ROBINSON 1977): *Phyllomyza* spec. (Milichiidae) on prey of *Nephila clavipes* (L.), *Conioscinella* spec. in the web of *Argiope argentata* (Fabricius). Best known, relatively, are the members of the genus *Microphor* (Microphoridae) with eight species and eight further species of related genera in Europe (PAPE 2010). Most of the *Microphor* species, if not all, are seen in association with spiders and their prey. They usually sit on the prey item while the spider is sucking on it. CHVALA (1986) stressed that MACQUART (1827) previously noted an association with spiders. *Megaselia scalaris* Loew (Phoridae) was found on the webs of *Tengella radiata* (Kulczynski) (EBERHARD et al. 1993).

Lepidoptera

Caterpillars of some lepidopteran families are known to feed on spider prey. POCOCK (1903) states that the larvae of *Batrachedra stegodyphobius* Walsingham (Batrachedridae) live in the communal web of a *Stegodyphus* species (Eresidae) in South Africa. According to Pocock pupation of the noctuid moth occurs in the spider web and the adult moths are seen fluttering about the web. ROBINSON (1977) reported the larvae of *Neopalthis madates* Druce (Noctuidae) living in the communal web of *Anelosimus eximius* Simon in Panama. The caterpillars of *Tallula watsoni* Barnes & McDunnough (Lepidoptera, Pyralidae) seem to live exclusively in the webs of *Anelosimus studiosus* (Hentz), where they eat dead and living leaves from the supporting tree or shrubs and attack or eat the spiders (DEYRUP et al. 2004). All these species are not only kleptoparasites but also inquilines which live in the web permanently.

Heteroptera

Among the bugs (Hemiptera-Heteroptera) there exist kleptoparasitic specialists in several families. *Arachnocoris* (Nabidae) is a genus which occurs with nine species (2-5 mm) in the Neotropical Region (Lopez-Moncet 1997). An upside-down position in the spider web is typical for this taxon. The different species were found in webs of Araneidae (*Micrathena*) (with sticky silk), Theridiidae (*Tidarren fordum* (Keyserling) (= *Tidarren sisyphoides* (Walckenaer)), *Anelosimus eximius* (Keyserling)) (sticky) as well as those of Pholcidae (*Physocyclus* sp.) (non-sticky silk). Strangely, specimens of *Arachnocoris trinitatis* Bergroth, one of the best studied species of the genus, are usually found in empty webs of the pholcid *Mesobolivar aurantiacus* (Mello-Leitao). It is hypothesized that the bug uses the web for catching prey and finding a mate (SEWLAL & STARR 2008). It is not clear whether the bug emptied the web by capturing and devouring the spider or by chasing it away.

The genus *Ranzovius* (Miridae) comprises at least four species which are associated with spiders (WHEELER & MCCAFFREY 1984). All specimens in this genus are very small (2–2.5 mm) and are found in orb webs as well as in sheet webs. *R. fennahi* Carvalho lives in large webs of the social *Anelosimus eximius* (Keyserling) while *R. contubernalis* Henry occurs in the communal webs of the social *Anelosimus studiosus* (Hentz). In the large spatial webs of the latter a lot of prey remnants are scattered throughout the web which attract pyralid larvae, cockroaches and ants which behave as scavengers. *R. californicus* (Van Duzee) consumes prey in the webs of *Hololena curta* (McCook) (Agelenidae). *R. agelenopsis* Henry can be found in high numbers in the webs of the common *Agelenopsis pennsylvanica* (C.L. Koch) where *R. contubernalis* can be found as well. *Agelenopsis* species are often common in shrubs and hedges. The webs of other common spider species in the same habitat, such as the linyphiid *Frontinella pyramitela* (Walckenaer) and various araneids (probably *Zygiella* species) were checked for the presence of *Ranzovius* but none were found (WHEELER & MCCAFFREY 1984). Apparently *Ranzovius* prefers *Anelosimus* and *Agelenopsis* for its kleptoparasitic practises.

In the Reduviidae the relatively common species *Reduvius personatus* L. has been found in webs of "house spiders", a name used in the U.S.A. for *Parasteatoda tepidariorum* (C.L. Koch) (AMYOT & SERVILLE 1843). There are a number of striking examples of kleptoparasites within the subfamily Emesinae (Reduviidae), viz. the genera *Eugubinus*, *Ploiaria*, *Emesa*, *Empicoris*, and *Stenolemus*. They all feed on the prey of the spiders the webs of which they invade. In the case of *Eugubinus araneus* Distant this was a theridiid (in Bombay) (DISTANT 1904), while

E. intrudans Distant and *E. reticolus* Distant were seen in webs of *Cyrtophora cicatrosa* (Stoliczka) (India) (DISTANT 1915). *Stenolemus* represents a transition to araneophagy.

More web-invading heteropteran species can be found in the Anthocoridae, viz., *Cardiastethus inquilinus* China & Myers in South Australia, in the web of a gregarious oxyopid (CHINA & MYERS 1929).

Species of the Plokiophilidae, with the genera *Plokiophila*, *Plokiophiloides*, *Lipokophila*, and *Embiophila* are found in the webs of Dipluridae and Tengellidae in the southern hemisphere (MCGAVIN 1993). The very small *Plokiophila cubana* (China & Myers) occurs on the webs of *Diplura macrura* (C.L. Koch) (Dipluridae) in Cuba. *Lipokophila eberhardi* Schuh and *L. tengella* Schuh were found on the webs of *Tengella radiata* (Kulczynski) (Tengellidae) (EBERHARD et al. 1993). According to CARAYON (1974) Plokiophilidae spend their whole life in the webs of spiders. They live there from egg stage to death. The egg is deposited on a thread in the spider's web and the young bug hatches immediately. *Plokiophiloides asolen* Carayon lives in webs of the social *Agelena consociata* Denis, while *P. balachowskyi* Carayon lives in webs of the social *Agelena republicana* Darchen. *P. biforis* Carayon was collected from webs of *Lathrothele catamita* (Simon) (Dipluridae). The reduviids *Themonocoris bambesanus* Carayon and two Anthocoridae (*Cardiastethus affinis* Poppius and *C. lateralis* Poppius) live there too.

When reduviid bugs live in a spider web these are free of kleptoparasitic spiders (LOPEZ-MONCET 1997). Possibly bugs live in spider webs because they are safe there from ants which are everywhere but hardly ever enter spider webs (LOPEZ-MONCET 1997).

Insects and spiders as predators on spiders

Araneae

For spiders any other spider is potential prey when it falls within the limits of its range of possibilities (size, danger, risk, defence of prey, etc.). Some spiders have made a habit of eating spiders of other species, a habit called "araneophagy". For cannibalism (occasional eating of specimens of the own species), see above.

Mimetidae are specialized predators on other spiders which they attack in the web of the prey by producing signals resembling those of an entangled insect or a potential mate wanting to pair, so-called "aggressive mimicry" (JACKSON & WHITEHOUSE 1986). From observations made by Bristowe (1958) it is clear that Mimetidae have very strong, paralyzing venom. Salticidae of the subfamily Spartaeninae are specialized in capturing spiders in their webs by stealthy approach combined with aggressive mimicry. The genus *Portia* is the best known genus (five species) which exploits this type of prey capture, but there are three other genera which show this type of behaviour as well, viz. *Brettus* (two species), *Gelotia* (one species), and *Cyrba* (two species) (WANLESS 1984). All these salticids share the characters of good vision with the ability to walk over sticky and non-sticky webs (JACKSON 1986). The pholcid *Pholcus phalangioides* ventures into the webs of other spiders and overwhelms the owner (JACKSON & BRASSINGTON 1987). Some Palpimanidae invade the web and lure the host out (HENSCHEL et al. 1992).

There are many examples of insects which are predators of spiders. The following examples are listed by order.

Heteroptera

Stenolemus species (Reduviidae, Emesinae) can be found in the surroundings of the spider webs which they penetrate to prey on the spider. *Stenolemus* are large, up to 1 cm overall body length, with long, thin legs. The 1990 catalogue of the Reduviidae of the world (MALDONADO CAPRILES 1990) listed 78 species, four of which are known to be predators on spiders. *S. arachniphagus* Maldonado-Capriles & Van Doesburg from Dutch Guiana (Surinam) was found in the communal web of *Anelosimus rupununi* Levi. They have peculiarly modified antennae which may be an adaptation to their habit of walking through webs (MALDONADO-CAPRILES & VAN DOESBURG 1966). *S. lanipes* Wygodzynski has been observed to eat juveniles of *Achaearanea tepidariorum* (C.L. Koch) (= *Parasteatoda t.*) (HODGE 1984). *S. giraffa* Wygodzynski (Australia) has a striking, elongate prothorax, hence its name. *S. edwardsi* Bergroth has been recorded as preying on young specimens of *Badumna* (Desidae) in Australia (Wignall & Taylor 2008). *Stenolemus bituberus* Stal was found in the webs of – and seen actually feeding on – spiders of the families Desidae, Pholcidae, Theridiidae, and Uloboridae. Most likely araneophagy will be found subsequently among the many other *Stenolemus* species known.

Neuroptera

The subfamily Mantispinae of the Mantispidae are predators of spider eggs. The front legs resemble those of the praying mantis, hence the name mantispid flies. They are fairly long, up to 5 cm. The stalked eggs are

deposited on the substratum. Different strategies are employed to reach the spider's eggs (REDBORG 1998). The larvae of one group of mantispids, the "boarders", attach themselves to a passing bee, beetle, or spider. The larva then rides along on the spider, usually curled around the pedicel, feeding itself with haemolymph fluid from the spider, acting as a leech. Their final destination is the egg cocoon or egg batch. When a mantispid larva has settled on a young spider it has to get on the newly emerging next instar of the spider when it moults. It may seek refuge temporarily in a book lung during the moulting process. They wait for the construction of the egg cocoon, slip into it, feed on the eggs and pupate in the cocoon or egg batch. In the other strategy, that of the "borers", the larva is attracted by spider silk and thus finds an egg sac and bores into it to feed on the eggs. Spiders which suffer from mantispid egg predation by spider boarders belong to a wide range of families of web builders as well as active hunters (REDBORG 1998), while the independent egg sac penetrators all feed exclusively on the eggs of hunting spiders.

Odonata

All Pseudostigmatidae ("Helicopter damsel flies") in which the adult feeding habits are known prey exclusively on web-building spiders. Gifted with very good vision they aim directly at the spider. Species showing this behaviour are *Mecistogaster linearis* (Fabricius), *M. modesta* Selys, *M. ornata* Rambur, *Megaloprepus coerulatus* (Drury), and *Pseudostigma accedens* Selys (CORBET 1999). *M. coerulatus* was seen preying on small *Argyrodes* spec. (Theridiidae) at a *Nephila* web (YOUNG 1980). *M. modesta* was seen at work near orb webs, as well as at the lampshade-shaped webs of pholcids.

Hymenoptera

Species from the Vespoidae, such as the hornet (*Vespa crabro* L.), and *Vespula* species capture spiders as food for their brood. Because the colonies of these social living insects are often very large the impact on the local spider fauna must be considerable. *Vespa crabro* acts as a regular kleptoparasite as well as predator on *Argiope bruennichi* (Scopoli) (Figs. 2-3).

Ants are about the largest and ever present group of predator insects, often occur in very high numbers in certain habitats and are known to bring all types of prey to their nests, among which spiders do not fail. I have not found any literature on the relative importance of spiders in the ants' diet.

Coleoptera

Carabid beetles are known to feed on spiders on agricultural fields, but no quantitative data are available.

Figures 2, 3: *Vespa crabro* in web of *Argiope bruennichi* steeling the spiders prey (2) (Photo Jeanette Hoek), and with remnant of *Argiope bruennichi* (3) (Photo Marcel Wasscher).

Figure 4: *Tromatobia ornata* on egg cocoon of *Argiope bruennichi*. Photo Gerben Winkel.

Parasites and Parasitoids

Egg parasitoids

Some Pimplinae (Hymenoptera, Ichneumonidae) are predators of spider eggs (*Gelis*, *Hemiteles*, *Tromatobia*, *Zaglyptus*, some Scelionidae) (RICHARDS 1977). The pimpline larva eats from the eggs in the spider's egg sac. Species of *Tromatobia* parasitize the egg sacs and adults of spiders. *Tromatobia* is a species-rich genus (FITTON et al. 1988). A striking example is *Argiope bruennichi* (Scopoli), a species which has spread relatively quickly under its own power and of which the egg cocoons are parasitized by *Tromatobia ornata* Gravenhorst (Fig. 4). The parasite may have travelled along with the spider when it spread over the Netherlands over the last 25 years.

True parasitoids

Among Hymenoptera, the Ichneumonidae are also parasitoids of adult insects and spiders. They paralyze their prey, place an egg and after hatching the larva feeds on it while it remains in a stable, paralysed condition (endoparasitoids); or they place an egg on the victim which then continues its normal life until it succumbs because it is slowly weakened by its uninvited ecto-parasitic guest.

Spider-wasps (Hymenoptera, Pompilidae) are specialized parasites of spiders. Their search for and capture of spider specimens is followed by a paralysing sting. The spider is then brought to a suitable place where it is burrowed, an egg is put on the spider, and the burrow is closed. The pompilid larva when full-grown pupates in the burrow. Most pompilid waps are polyphagous and hunt for spiders in general or specialize on webspiders. Some are monophagous, at least regionally, such as *Homonotus sanguinolentus* Fabricius which exclusively hunts for *Cheiracanthium erraticum* (Walckenaer) (Miturgidae) which is then left in its own silken nest (NIELSEN 1936). There are exceptions in this sequence. *Eoferreola rhombica* (Christ) parasitizes on *Eresus sandaliatus* (Martini & Goeze) (Eresidae). This spider lives in a burrow with a cribellate web above the entrance. Having located the spider in its burrow the wasp enters, paralyzes the spider, places its egg on the animal and leaves the burrow without closing it. It does not make a burrow of its own (HAUPT 1927). Neither does *Aporus unicolor* Spinola, which locates *Atypus* (Atypidae) in its burrow and leaves it there after having paralyzed it and provided an egg. *Ceropales* species (Pompilidae) are known as kleptoparasites of other Pompilidae in that they follow other pompilid wasps with prey and put an egg on the prey just before the prey is buried by the true hunter (OEHLKE & WOLF 1987).

Within the Ichneumonidae the Pimplinae comprise the spider-ectoparasitoids of the *Polysphincta* group of genera of which we often see the larva externally on the abdomen (RICHARDS 1977). Species of the *Polysphincta* genus-group of the Pimplinae attack spiders. They first immobilize the spider, then put an egg on the spider, usually on the abdomen. The spider regains consciousness and leads a normal life until the larva is full-grown and pupates in the body of the dead spider. Many genera are distinguished, such as *Dreisbachia*, *Schyzopyga*, *Polysphincta*, *Acrodactyla*, *Synarachna*, and *Zatypota* (FITTON et al. 1988; GAULD et al. 2006).

A curious phenomenon in this respect is a procedure which is called "manipulation of the host behaviour". When the larva of *Hymenoepimecis argyraphaga*

Gauld (Ichneumonidae) is ready to pupate it stimulates the host spider *Plesiometa argyra* (Walckenaer) (= *Leucauge argyra* (Walckenaer)) (Tetragnathidae) just before it will die to produce a hub for a new web and repeat this over and over again, thus fabricating a "cocoon web" for its own parasitoid wasp (EBERHARD 2000, 2001), this process probably stimulated by chemicals brought into the host's body. I am not aware of any other cases of manipulation of behaviour by parasitoids of spiders.

Within the Apoidea, the Crabronidae or digger wasps, comprise species which specialize on spiders and show a behaviour equivalent to that of the Pompilidae. Species of the genus *Miscophus* hunt for small spiders, and *Trypoxylon* species capture larger spiders, which they put in a cell and close off with mud.

Diptera

When the larvae of Acroceridae (Cyrtidae, Oncodidae) hatch they try to find a spider and climb on it, enter the book lungs and develop inside the abdomen. The spider dies when the parasitoid is full-grown and pupates. More than 500 species are known worldwide, mostly in the tropics. Recent additional data of acrocerid infestations in the Nearctic Region are given by LARRIVÉE & BORKENT (2009).

Discussion

Spiders are strongly armed, well-equipped predators: they have fangs to inject their venom, different types of silk for their webs – sticky or cribellate – and methods to wrap up their victims very quickly, and they have very short reaction time. For spiders the transition from hunting to invading a strange web, to kleptoparasitism, to becoming predator of a non-specific spider species, or to cannibalism, is nearly a continuum. The driving force in all instances is the search for food to meet the requirements of the individual's energy balance. Food shortage will force spiders to eat individuals of their own kind. Other spiders, being live objects, are always on the menu. Once it is possible for an individual spider to enter a strange web unobserved or with misleading behaviour the intruder can benefit from available food (kleptoparasitism), protection from other organisms which cannot enter the web (such as ants), or capture the owner by surprise (araneophagy). There are many examples of insects that follow the same strategies. There are also many invertebrates that have found ways and means to master spiders: they have won the arms race.

It is clear that spider kleptoparasites benefit from using the prey collected by others. They do not have to invest in silk for webs, venom, or energy needed for hunting, jumping and overwhelming, while silk production for wrapping can be omitted. One may expect that exclusively kleptoparasitic spider species even have lost their capacity to produce venom, while the glands for silk production may have undergone reduction. The kleptoparasitic spider also gains protection from other predators, such as the ever present ants, which, however, have been observed only in a few spider species to enter the web. For the host spider the stealing of food means loss of invested energy but for a larger host (*Nephila*, communal *Anelosimus*) this may be negligible, also because the kleptoparasites often eats from smaller prey for which the web owner has no interest.

Aggression towards kleptoparasites by the web owner is nearly always negligible too, partly because of size differences (small kleptoparasites in the webs of larger species), partly because of subdued aggression (spiders in communal webs). Kleptoparasitism appears to be not so rare a phenomenon, although the number of spider species which employ this feeding behaviour is relatively restricted as far as we know now. The number of insects that play a kleptoparasitic role in relation with spiders probably is larger than we know now. It may be expected that observations of spiders in their natural environment may reveal more kleptoparasitic relationships, especially in the acalyptrate Diptera and reduviid Heteroptera.

Spiders are not defenceless against predators. They can defend themselves with their chelicerae and fight back, but against most stinging Hymenoptera they seem to hardly have a chance, although we do not know how many attempts by Ichneumonidae, Crabronidae, and Pompilidae meet with failure. Spiders can drop from the web, change colour when hitting the ground, run away, hide in self spun cells, or flee to the other side of the web, putting the web between himself and predator (JACKSON et al. 1993). However, their chances of defence against predators which successfully deploy "aggressive mimicry" seem to be very slight. In the described cases the victim spiders were lured within striking distance of the predators "on perfidious pretexts" and the victim had very slight chances to escape. Apparently the "behavioral" arms race has been won by the predators, although we do not register where such methods are developing right now and have a lower percentage of successful attempts. It is difficult to detect evolution at work and

understand the direction the selective forces might move into.

If we look at the orders of invertebrates (other than spiders) which have developed scavengers, kleptoparasites, or predators, and parasitoids of spiders we must conclude that the largest order, the Coleoptera with 359,891 described species, has hardly developed any (carabid beetles can feed on spiders on arable land if no other food is available), that the Diptera (152,244) have some kleptoparasites among them but are under-represented as to predators (none) and parasitoids (only one family). Lepidoptera (156,793 species) are represented with noctuid kleptoparasites, but this feature seems to be rather exceptional in the order. The Odonata are a small order (5,680 species) of which only few genera have developed into spider predators. By far the most kleptoparasites are found among the Hemiptera (100,428 species), while some have become predators. The largest number of general predators, parasites and parasitoids are found in the Hymenoptera (144,695 species), which all possess poison glands and thus are able to overwhelm and/or parasitize spiders. They have developed a weapon of their own and are clearly ahead in the arms race. (All data on species numbers after ADLER & FOOTTIT 2008.)

Reflections

Interactions as brought together and discussed in this paper are of importance for understanding the biology of the species, of spiders as well as of the many insects involved. Discovering new relationships and interactions will help us to understand the many interesting behavioural patterns and food chains which exist in the invertebrate world. They illuminate an important aspect of the "web of life" and demonstrate the intricacies of food chains. It is clear that this asks for collecting observations in the field more than collecting specimens. Pitfalls and canopy fogging yield specimens and give insight in the composition of the fauna but they do not help us to find patterns of behaviour, parasitic relationships or food chains. This paper is meant to stimulate the observing type of invertebratologists who sits down amidst the invertebrates at work and tries to discover the patterns of interactions between organisms, the way organisms react to each other.

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Arachnologische Mitteilungen 40: 65-79 Nuremberg, January 2011

Endemic harvestmen and spiders of Austria (Arachnida: Opiliones, Araneae)

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doi: 10.5431/aramit4008

Abstract: A comprehensive overview of plant, fungus and animal species of Austria revealed a total of 748 endemic and subendemic species, including, 11 harvestman and 46 spider species. Altogether two endemic harvestmen *(Nemastoma bidentatum relictum, Nemastoma schuelleri)* and 8 endemic spiders (*Abacoproeces molestus, Collinsia (caliginosa) nemenziana, Mughiphantes severus, Mughiphantes styriacus, Pelecopsis alpica, Scotophaeus nanus, Troglohyphantes novicordis, Troglohyphantes tauriscus*), beside 9 subendemic harvestman and 38 subendemic spider species have been recorded from Austria. Hot-spots of endemism in the Eastern Alps are the north-eastern (Ennstaler Alps) and southern Calcareous Alps (Karawanken, Karnische Alps) and the Central Alps (Hohe Tauern, Gurktaler Alps, Ötztaler and Stubaier Alps). Most of the endemic arachnid species occur from the nival down to the montane zone. Important habitats are rocky areas, caves and woodlands. High absolute numbers and percentages of endemics can be found within the harvestman families Cladonychiidae, Ischyropsalididae and Nemastomatidae and in the spider genera *Lepthyphantes* s. l. and *Troglohyphantes*. The conservation status of these highly endangered taxa – 85 % of the spider species and 100 % of the harvestman taxa are endangered in Austria – is poor.

Key words: conservation, Eastern Alps, endangering, endemism, ice age, massifs de refuge, nunataks, red list, subendemics, protection, vertical distribution

Zoogeography appears to be one of the most amusing and stimulating of the natural sciences: every few years its fundamental concepts change and one can begin anew.
Paolo Marcello BRIGNOLI (1983: 181)

The so-called Eastern Alps belong to the 30-35 million year old European Alpine system, and are largely contained within the national borders of Austria. Despite intensive research efforts by several Austrian zoologists in the past, like Rudolf Heberdey, Karl Holdhaus, Herbert Franz and Heinz Janetschek or the German Gustaf de Lattin as well as more recently renowned „Alpine-arachnologists" like Konrad Thaler and Jürgen Gruber, a comprehensive faunal catalogue for the region is lacking.

A recent study, co-ordinated by the Environment Agency Austria (Umweltbundesamt), aimed to fill this deficit. A comprehensive overview of plant, fungus and animal species, whose range lies entirely (endemics) or predominantly (subendemics) within the political borders of Austria, has now been completed (RABITSCH & ESSL 2009). Altogether 748 (sub)endemic animal and plant species have been identified. Among the 548 animal species in Austria 10 pseudoscorpion (7 endemic, 3 subendemic) (MAHNERT 2009), 11 harvestman (KOMPOSCH 2009a) and 46 spider species (KOMPOSCH 2009b) can be found (Fig. 1, 2). Scorpions (KOMPOSCH 2009c) and palpigrades (CHRISTIAN 2009) include no real (sub)endemic species of Austria, whereas 10 oribatid mites (SCHATZ & SCHUSTER 2009) are classified as endemic and subendemic; many more oribatids are pseudoendemics, i. e. the current taxonomy of faunistic knowledge is not sufficient and a wider distribution is assumed.

So why is it important to publish these data in addition to the endemics book? This is done for the following reasons: first the endemics book is of regional distribution, mainly spread in Austria, and due to the small print run it will soon be sold out (compare BLICK 2009). Second it is written in German, and for the relevant chapters even an English abstract is missing. The present publication closes this gap for the arachnological section. Furthermore it expands and updates the knowledge of the two treated arachnid groups.

Material and Methods

This paper deals with species and subspecies, whose ranges lie entirely (endemics) or predominantly (subendemics) within the political borders of Austria.

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submitted: 19.1.2010, accepted: 20.4.2010; online: 10.1.2011

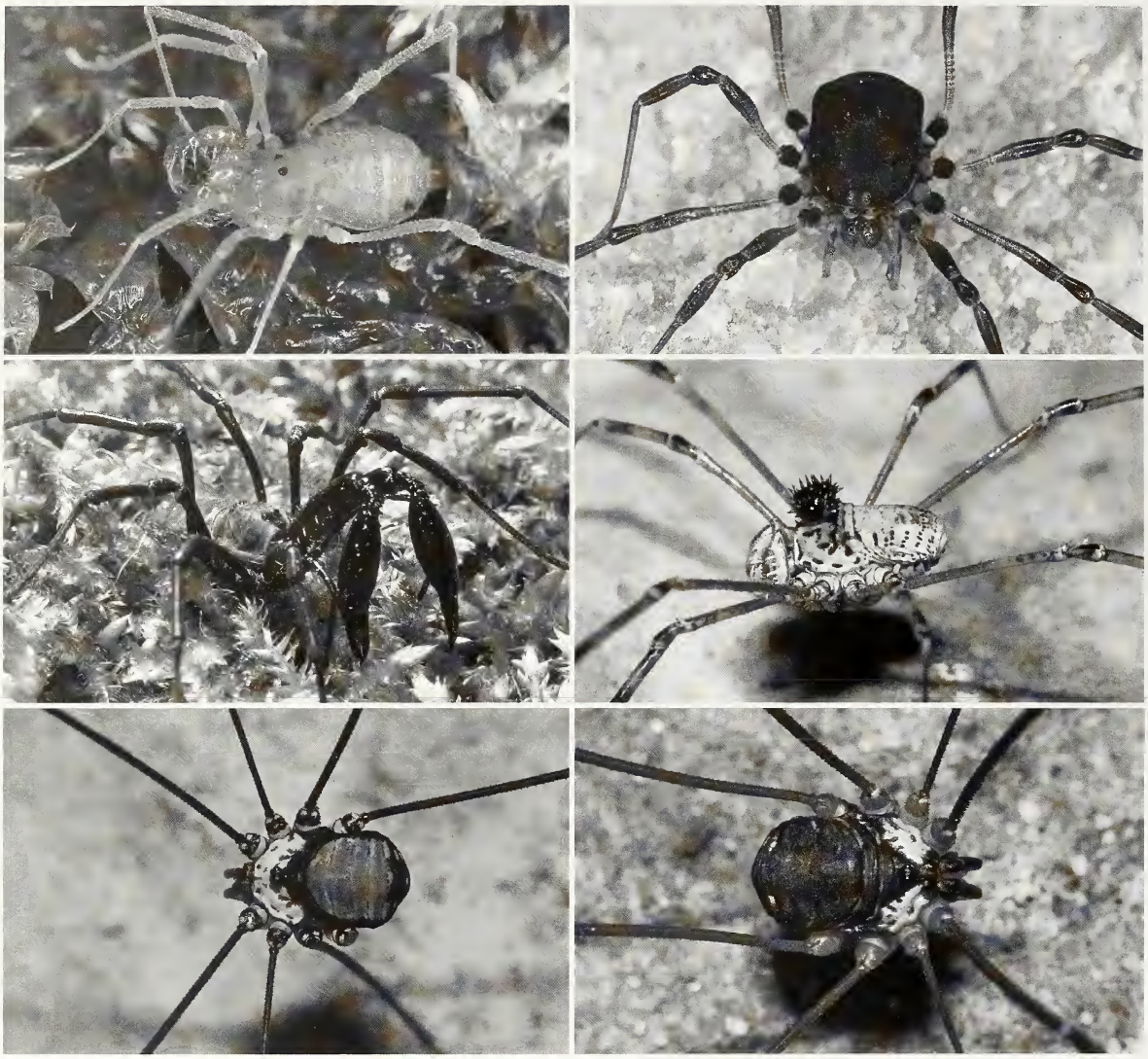

Figure 1: Habitus of endemic and subendemic harvestmen of Austria. From left to right and from the top downwards: *Holoscotolemon unicolor, Paranemastoma bicuspidatum, Ischyropsalis kollari, Megabunus armatus, Leiobunum roseum, Leiobunum subalpinum.*

Subendemics are defined in this context as taxa with more than 75 % of their total range within Austria or if they are local or regional endemics with less than 10 known localities or if their area is restricted to less than 1000 km^2 respectively with less than 75 % of their total range in Austria (RABITSCH & ESSL 2009).

All available, published and unpublished, data on endemic and subendemic harvestmen and spiders have been collected, reviewed, geographically located, digitised and stored in a private database (data base ÖKOTEAM). Altogether more than 2250 data-sets were analysed (Araneae: 1050, Opiliones: 1200). The distribution maps (see appendix) – showing the natural zones as well as the political borders of the federal countries – have been printed by the Environment Agency Austria (UBA). All photos were taken by the author.

Results

The geographical localisation and digitalisation of all available data facilitated the present drawings of distribution maps (appendix 1, 2) and – for the first time – the clear identification of centres and hotspots of faunal endemism within the Eastern Alps.

A complete list of all endemic and subendemic harvestman and spider taxa is given in table 1, a selection of habitus photographs is presented in figure 1. Altogether two endemic (*Nemastoma bidentatum*

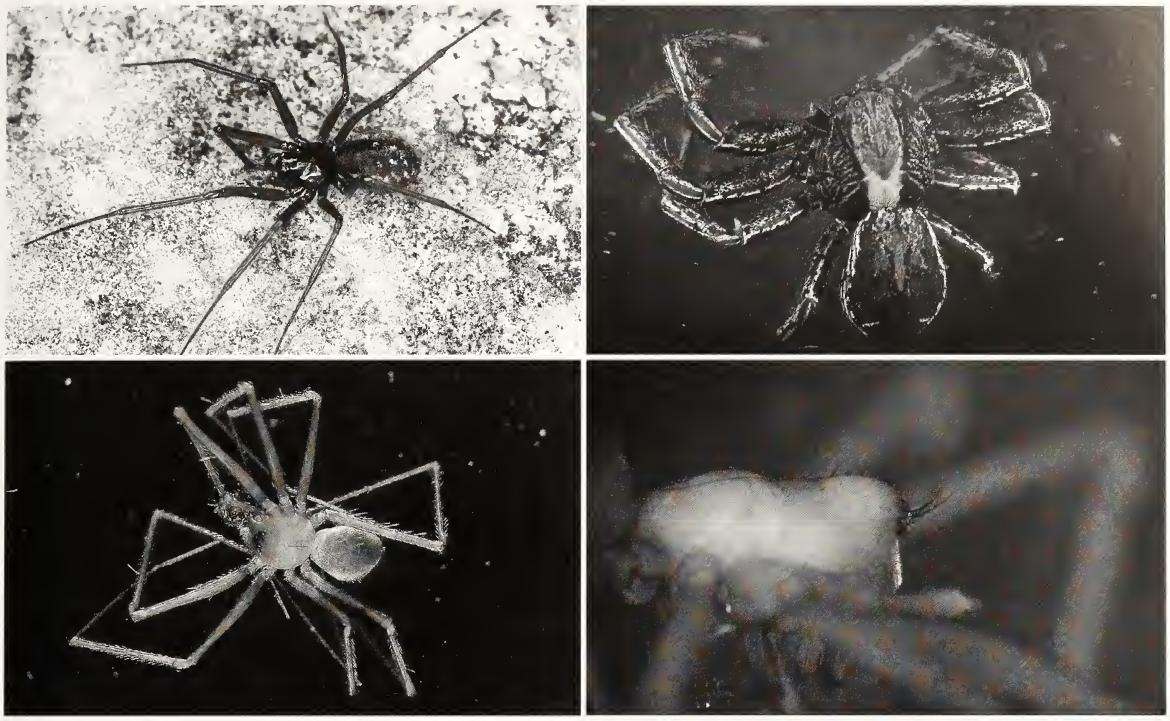

Figure 2: Habitus of endemic and subendemic spiders of Austria. From left to right and from the top downwards: *Mughiphantes variabilis, Xysticus secedens, Troglohyphantes tauriscus, Troglohyphantes noricus*.

relictum, Nemastoma schuelleri) and nine subendemic harvestmen are recorded from Austria (table 1, appendix 1). The spider fauna shows eight endemic (*Abacoproeces molestus*, *Collinsia* (*caliginosa*) *nemenziana*, *Mughiphantes severus*, *Mughiphantes styriacus*, *Pelecopsis alpica*, *Scotophaeus nanus*, *Troglohyphantes novicordis*, *Troglohyphantes tauriscus*) and 38 subendemic species (table 1, appendix 2). Therefore a total of 57 subendemic and endemic harvestman (11) and spider (46) species can be found within the Austrian Republic. Regarding the main vertical distribution of Opiliones and Araneae in the Eastern Alps the colline zone (115 up to ca. 250-400/500 m) harbours 2 harvestmen and 4 spider species, the submontane (up to ca. 350-500/700 m) 3 / 9, the montane (up to ca. 1500-2000 m) 10 / 21, the subalpine (up to ca. 1800-2100 m) 8 / 23, the alpine (up to ca. 2500-2800 m) 3 / 18, and the nivale zone (up to 3798 m) 1 / 6 species. Of the (sub)endemic taxa, 39 spider species (85 %) are "Critically Endangered" up to "Vulnerable" and two species (4 %) are placed in the category "Data deficient" (KOMPOSCH in press b). All 11 harvestman taxa are vulnerable or endangered in Austria (KOMPOSCH 2009d).

The horizontal distribution of arachnids shows major differences between the different natural areas in Austria. Rich in endemic spiders and harvestmen are the mountainous federal states of Styria (St), Carinthia (C), Tyrol (T) and Salzburg (S). MAURER & HÄNGGI (1990) pointed out, that endemics of the Northern Alps mostly show bigger areas than south-alpine ones. Concerning the fauna of the whole Alpine arc this is definitively correct. With respect to the distribution maps of Austrian (sub)endemics it could hardly be verified, as the political borders of Austria comprise a much bigger area of the Northern, as opposed to the Southern, Alps.

Discussion

The number of endemic and subendemic arachnids within Austria is remarkably high and differs widely in the nine federal states (Bundesländer). Centres of arachnological and zoological diversity and endemism are, within the entire Alps, the Southern Calcareous Alps with their peak in the south-western parts (Mercantour National Park and Alpi Marittime NP) (MAURER & THALER 1988). The hotspot of arachnological endemism in Austria is situated in the Eastern Alps. Following the definitions of subendemism of RABITSCH & ESSL (2009) the arachnological hotspots in Austria are the central Hohe Tauern (C, S, T) and the Gurktaler Alps (C, S, St), but also the

Table 1: List of endemic (E), subendemic (S), and pseudoendemic (P) harvestmen (Opiliones) and spider (Araneae) species of Austria, related to the altitudinal zones of their main occurrence in the area (colline to nivale). RLA = Red List of endangered harvestmen and spiders of Austria (KOMPOSCH 2009d, KOMPOSCH in press). Categories of endangerment used: LC = Least Concern, NT = Near Threatened, DD = Data Deficient, VU = Vulnerable, EN = Endangered, CR = Critically Endangered. * *Tapinocyba affinis* is endemic to the alpine mountainous system (THALER 1999). The subspecies *orientalis*, although not clearly shown up to now, seems to have a wider distribution in Slovakia, Czech Republic and Germany (MILLIDGE 1979, KOMPOSCH 2009b, Blick in litt.); in this case it would lose the subendemic-status in Austria.

	family	taxon	E/S	RLA	colline	submontane	montane	subalpine	alpine	nival
		Opiliones (harvestmen)								
1	Cladonychiidae	*Holoscotolemon unicolor* Roewer, 1915	S	EN	1	1	1			
2	Nemastomatidae	*Mitostoma alpinum* (Hadzi, 1931)	S	EN				1	1	
3		*Nemastoma bidentatum relictum* Gruber & Martens, 1968	E	EN			1	1		
4		*Nemastoma schuelleri* Gruber & Martens, 1968	E	EN		1	1	1		
5		*Paranemastoma bicuspidatum* (C. L. Koch, 1835)	S	EN			1	1		
6	Ischyropsalididae	*Ischyropsalis hadzii* Roewer, 1950	S	EN			1			
7		*Ischyropsalis kollari* C. L. Koch, 1839	S	VU	1		1	1	1	
8	Phalangiidae	*Megabunus armatus* (Kulczynski, 1887)	S	EN			1	1	1	1
9		*Megabunus lesserti* Schenkel, 1927	S	VU			1	1		
10	Sclerosomatidae	*Leiobunum roseum* C. L. Koch, 1839	S	EN		1	1			
11		*Leiobunum subalpinum* Komposch, 1998	S	VU			1	1		
		Araneae (spiders)								
1	Linyphiidae	*Abacoproeces molestus* Thaler, 1973	E	CR			1			
2		*Centrophantes roeweri* (Wiehle, 1961)	S	EN		1	1			
3		*Collinsia (caliginosa) nemenziana* Thaler, 1980	E	VU				1		
4		*Diplocephalus rostratus* Schenkel, 1934	S	EN						1
5		*Incestophantes kotulai* (Kulczynski, 1904)	S	VU					1	
6		*Meioneta alpica* (Tanasevitch, 2000)	S	DD				1		
7		*Meioneta ressli* Wunderlich, 1973	S	VU				1		
8		*Metopobactrus nodicornis* Schenkel, 1927	S	EN					1	
9		*Micrargus alpinus* Relys & Weiss, 1997	S	VU				1		
10		*Mughiphantes armatus* (Kulczynski, 1905)	S	VU						1
11		*Mughiphantes rupium* (Thaler, 1984)	S	CR					1	
12		*Mughiphantes severus* (Thaler, 1990)	E	CR					1	
13		*Mughiphantes styriacus* (Thaler, 1984)	E	CR					1	
14		*Mughiphantes triglavensis* (Miller & Polenec, 1975)	S	EN				1	1	
15		*Mughiphantes variabilis* (Kulczynski, 1887)	S	NT				1	1	1
16		*Palliduphantes montanus* (Kulczynski, 1898)	S	LC			1	1		
17		*Pelecopsis alpica* Thaler, 1991	E	CR					1	
18		*Scotinotylus clavatus* (Schenkel, 1927)	S	EN			1	1		
19		*Silometopus rosemariae* Wunderlich, 1969	S	VU				1	1	
20		*Styloctetor austerus* (L. Koch, 1884)	S	VU					1	1
21		*Syedra apetlonensis* Wunderlich, 1992	S	CR	1					
22		*Tapinocyba affinis orientalis* Millidge, 1979	S*	NT			1	1		
23		*Tenuiphantes jacksonoides* (Van Helsdingen, 1977)	S	NT			1	1	1	
24		*Troglohyphantes fagei* Roewer, 1931	S	VU				1	1	

	family	taxon	E/S	RL A	colline	submontane	montane	subalpine	alpine	nival
25		*Troglohyphantes karawankorum* Deeleman-Reinhold, 1978	S	CR			1	1		
26		*Troglohyphantes latzeli* Thaler, 1986	S	CR		1	1			
27		*Troglohyphantes noricus* (Thaler & Polenec, 1974)	S	VU	1	1	1			
28		*Troglohyphantes novicordis* Thaler, 1978	E	CR		1				
29		*Troglohyphantes subalpinus* Thaler, 1967	S	VU		1	1	1		
30		*Troglohyphantes tauriscus* Thaler, 1982	E	EN			1	1		
31		*Troglohyphantes thaleri* Miller & Polenec, 1975	S	VU		1	1	1		
32		*Troglohyphantes typhlonetiformis* Absolon & Kratochvil, 1932	S	CR		1	1			
33	Tetragnathidae	*Pachygnatha terilis* Thaler, 1991	S	EN		1	1			
34	Lycosidae	*Arctosa renidescens* Buchar & Thaler, 1995	S	EN				1	1	
35		*Pardosa giebeli* (Pavesi, 1873)	S	VU					1	1
36		*Pardosa saturatior* Simon, 1937	S	VU			1	1	1	
37	Agelenidae	*Tegenaria mirifica* Thaler, 1987	S	CR			1			
38	Hahniidae	*Cryphoeca lichenum lichenum* L. Koch, 1876	S	NT			1	1		
39		*Cryphoeca lichenum nigerrima* Thaler, 1978	S	EN				1	1	
40	Gnaphosidae	*Haplodrassus aenus* Thaler, 1984	S	EN		1	1			
41		*Haplodrassus bohemicus* Miller & Buchar, 1977	S	CR	1					
42		*Scotophaeus nanus* Wunderlich, 1995	E?	EN	1					
43		*Zelotes zellensis* Grimm, 1982	S	VU			1	1		
44	Philodromidae	*Philodromus depriesteri* Braun, 1965	S	DD			1			
45		*Thanatus firmetorum* Muster & Thaler, 2003	S	VU				1	1	1
46	Thomisidae	*Xysticus secendens* L. Koch, 1876	S	VU			1	1	1	

Ötztaler and Stubaier Alps (T) as well as the Koralpe (C, St) (all Central Alps), the Gesäuse National Park (Ennstaler Alps, Northern Calcareous Alps, St) and in particular the Karawanken (Southern Calcareous Alps, C) with their massifs de refuge, marking the margin of the Würm-ice-shields (Fig. 3). Regions outside the Alps are poor in endemics. For spiders and harvestmen a maximum of 12 taxa per grid-cell was found in Austria. Concerning all animals, the maximum was 46 taxa in a grid cell in the Gesäuse NP (St). The Hochobir (Fig. 4) in the Karawanken (Southern Calcareous Alps, C) came second with 41 endemic taxa. A comparison between the arachnological hotspots (Fig. 5) and these of the whole fauna (RABITSCH & ESSL 2009: 882) reveals a quite similar picture. Differences can be found in the araneological hotspot in the Ötztaler and Stubaier Alps, intensively explored by Konrad Thaler and his students, and – probably a methodical artefact – the comparatively low frequency in the eastern parts of the Northern Calcareous Alps (Styria, Upper and Lower Austria). Regarding a wider definition of subendemism the Austrian number one would be the Southeastern Calcareous Alps with the Karawanken and Steiner Alps at the borderline between Carinthia/Austria and Slovenia, followed by the Karnische Alps, marking the border between Carinthia/Austria and Italy.

Without attempting to explain the origin of these endemics in detail, I would like to point out three main reasons for the richness of the small-scale distributed species in the Alps:

1) The recent climate history with large-scale expansion of the last ice-shields (Fig. 3 is of importance to understand today´s distribution ranges. Like other zoogeographers, DE LATTIN (1967) previously pointed out that the geological event with the strongest influence on the Holarctic faunas was irruption by the Pleistocene ice-ages. HOLDHAUS

(1954) wrote about the "rettungslose Vernichtung" [desperate devastation] of the Alpine fauna by the glaciations.

2) The Alpine inhabitants were pushed towards refugia by the glaciations (e.g. BRIGNOLI 1983, WEISS & FERRAND 2007), then underwent evolutionary processes and post-glacial re-immigration over both short and long distances (HOLDHAUS 1954, JANETSCHEK 1956, THALER 2003).
3) Survival was possible in massifs de refuge, i.e. unglaciated massifs at the periphery of the ice shields (e.g. Fig. 3), in caves and – quite rarely – on inner Alpine nunataks (MAURER & HÄNGGI 1990, HOLDEREGGER & THIEL-EGENTER 2009). Nunataks are steep mountain peaks free of ice, which appear through the ice crust.

Due to the particular forms of glaciation (Fig. 3), survival and re-wandering processes in the Eastern Alps the diversity of endemic and subendemic spiders and harvestmen shows a South-North and an East-West decline (cf. MUSTER 2001, 2002).

Most of the endemic arachnid species occur from the alpine down to the montane zone (table 1). The most important habitats are rocky areas, caves and woodlands. High absolute numbers and percentages of endemics can be found within the soil-inhabiting harvestman-families Cladonychiidae, Ischyropsalididae and Nemastomatidae and the spider-family Linyphiidae (*Lepthyphantes* spp. s. l. and *Troglohyphantes* spp.). Beyond these linyphiid taxa MAURER & HÄNGGI (1990) list *Coelotes*, *Cryphoeca*, *Cybaeus*, *Nesticus*, dysderids and leptonetids.

The threat status of endemic spider- and harvestman-species in Austria is in general high. The major threats are caused by forestry (old-growth forests are being replaced by common spruce monocultures), hydraulic engineering (large Alpine valleys are flooded and changed to hostile reservoirs), agriculture (intensification and biocide use) and tourism (devastating high Alpine and mountainous areas for building and expanding ski-regions; a big problem is the enormous need for water for ski cannons, which leads to the construction of water reservoirs, water diversion and the destruction of spring communities, brooklets and brooks). Furthermore climate warming leads to habitat loss and endangers cold stenothermic species inhabiting rather low peripheral mountain chains of the Alps, which were not glaciated during the Pleistocene; DIRNBÖCK et al. in press). Despite these various hazardous impacts on sensitive habitats and their species, endemic arachnids and insects are so far not protected by Austrian laws. The coverage of the distribution of endemics by nature reserves is rather poor. Firstly none of the Austrian nature conservation areas or National Parks has been established up to now in response to a high or even outstanding diversity among endemic invertebrates. Not more than 10 % of

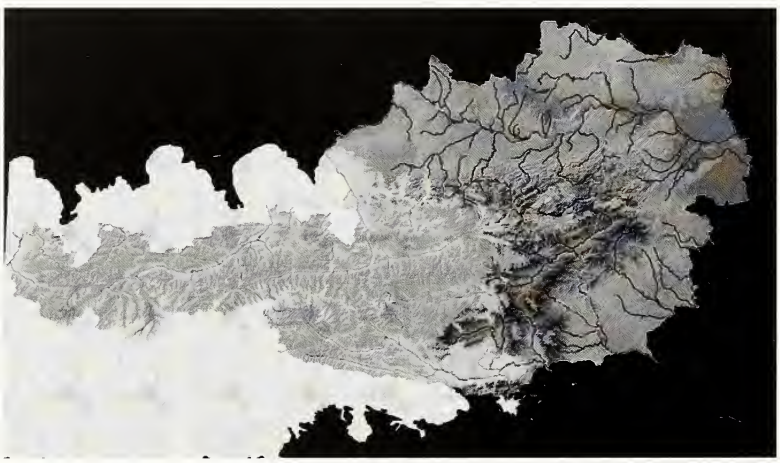

Figure 3: The eastern Alps at maximum glaciation during the last Ice Age (Würm): orography and political borders of Austria (modified after VAN HUSEN 1987, RABITSCH & ESSL 2009)

Figure 4: The Hochobir, an impressive peak and massif de refuge within the Karawanken (Southern Alps, Carinthia), is a well known hot spot of endemic arachnids.

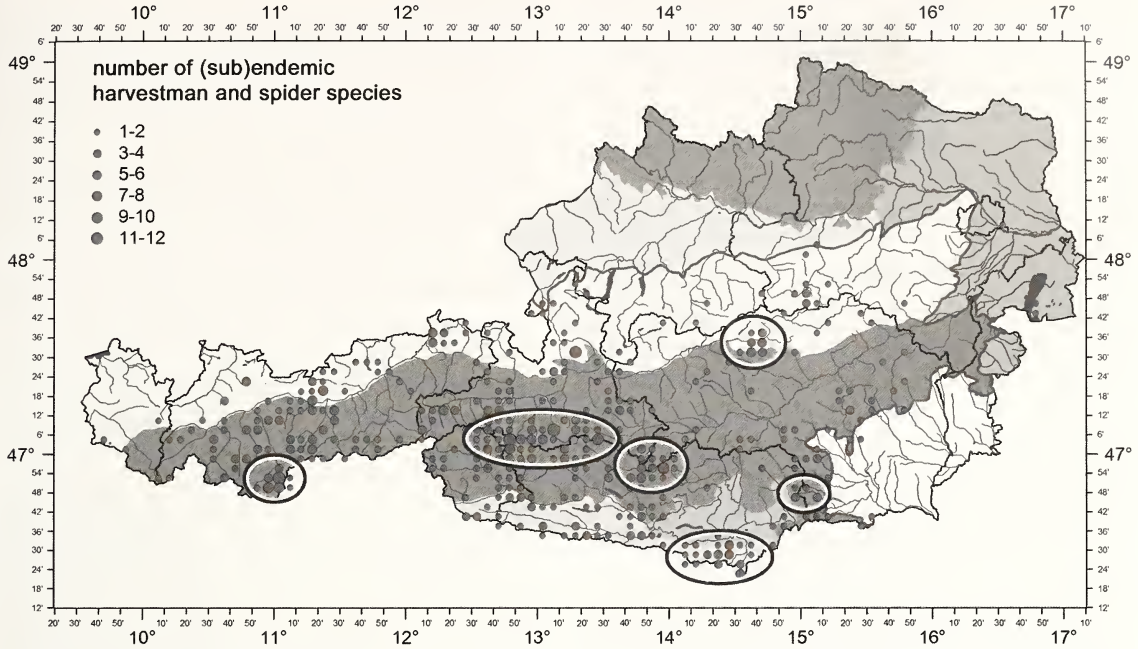

Figure 5: Cumulative distribution map showing all endemic and subendemic spiders and harvestmen in Austria (modified after KOMPOSCH 2009b). The main hotspots of arachnological endemism are encircled by rings and ovals.

the 16 quadrants with the highest number of endemic animals in Austria are covered by nature conservation areas. Secondly the coverage of large parts of the country by Natura-2000-areas rules out protection of the endemic species inside these areas as they are not regarded as conservation objects by the European Union.

It is quite astonishing that comparative data on endemic arachnids from other central European countries are missing or weak. Therefore a comparison to the Austrian results is hardly possible. This highly unsatisfactory situation is in need of change.

Available data refer to Romania: TATOLE (2006) carried out a zoogeographical analysis of the 961 hitherto registered spider species and identifies about 6 % as endemic. The spider fauna of Bulgaria is represented by 975 species, including "76 species (10 %) established in Bulgaria (35 species) and other territories of the Balkan Peninsula (41 species)" (DELTSHEV 2005: 309). Following this author, this phenomenon can be attributed to the relative isolation of the mountains compared with the lowlands in the context of paleo-environmental changes since the Pliocene. MAURER & HÄNGGI (1990) disclose in their catalogue of Swiss spiders a value of 7 % of merely alpine species – i.e. just partly endemic or subendemic taxa of Switzerland. The spider fauna of the Caucasus, comprising Armenia, Azerbaijan and Georgia as well as parts of the Iran, Turkey and Russia, is poorly known; the value of endemic spiders is 22 % (> 226 endemics from a total of 1022 species) (MARUSIK et al. 2006).

Conclusions

The presented results provide a valuable basis for both zoogeographical inferences involving glacial refugia and postglacial re-colonisation of the fauna of the Alps as well as conservation planning in Austria.

Although known from other animal groups, the high diversity of endemic spiders and harvestmen from the Gurktaler Alps and the Gesäuse National Park (KOMPOSCH 2010) was surprising. Further faunistic and taxonomic work especially in these areas should bring forward new and undescribed species. As pointed out before, the status of subendemism strongly relates to its definition. A second step towards the recording and documentation of the subendemic fauna of Austria – and the endemic fauna of the Alps – is urgently needed. From the conservation perspective it is not acceptable to pay attention merely to species with a 75 % area-quotient within national borders. Taking into account the fact that several rare, small scale-distributed and endangered species share their area equally within two or three countries (e.g. within

the south-eastern Alps: Slovenia, Italy and Austria), only a percentage of about 20 clearly leads to a main distribution within each country and consequently to a main responsibility for each country.

The need for action is great, and the time pressure due to habitat destruction and climate warming is high. The following four steps should be rapidly undertaken:

1) Clarification of targets and general conditions of a national and international protection concept, including basic research, politics, protection measures, university training and public relations (KOMPOSCH in press a).
2) Identification and prioritisation of endemic taxa (local, regional and endangered endemics) and regions (hotspots of endemism) – with continuative and representative mappings – with a high need for protection.
3) Drafting of specific protection measures, showing deficits of knowledge and priorities of research. Stopping the loss of organismic biologists and specialists able to identify a species.
4) Implementation of the protection concept (e.g. KLAUSNITZER 2010) (anchoring the protection of endemics in federal conservation laws as well as in the FFH-directive of the European Union), accompanied by long-term monitoring and readjustment of measures.

Conservation efforts must focus on these unique treasure of our Alpine fauna.

Ackowledgements

For arachnological data and help I am deeply grateful to Konrad Thaler (†), Jürgen Gruber and Albert Ausobsky. Thanks for data, literature, fieldwork and intensive discussions to Franz Essl, Thomas Frieß, Werner Holzinger, Barbara Knoflach, Brigitte Komposch, Jochen Martens, Christoph Muster, Tone and Ljuba Novak, Wolfgang Paill, Axel Schönhofer and Reinhart Schuster. Financial support came from the Umweltbundesamt Vienna (project-support), the Österreichische Forschungsgemeinschaft and the Styrian Government (both support of the congress participation in Alexandroupolis 2009) and technical support from Wolfgang Rabitsch. Big thanks go to the two anonymous reviewers, Jason Dunlop for improving the English, Theo Blick and Oliver-D. Finch for discussion und valuable comments and to Maria Chatzaki for her patience with the manuscript.

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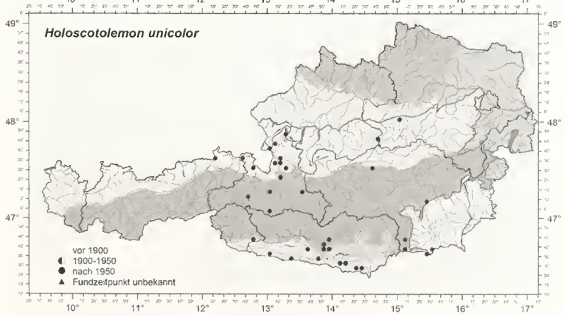
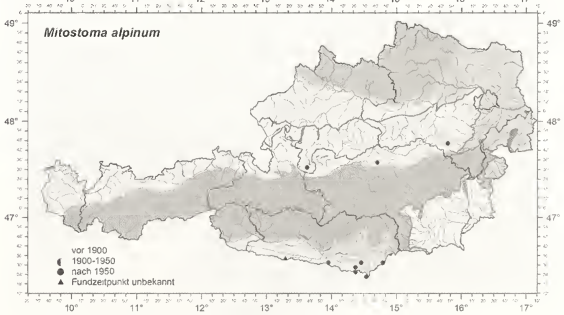
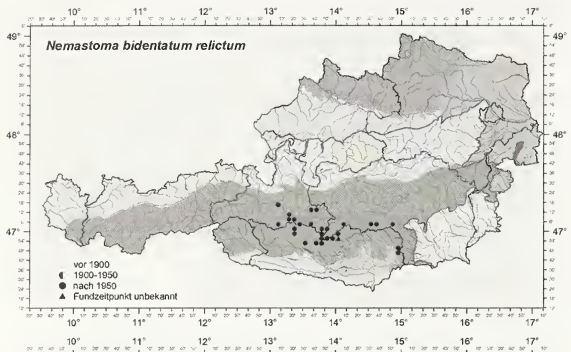
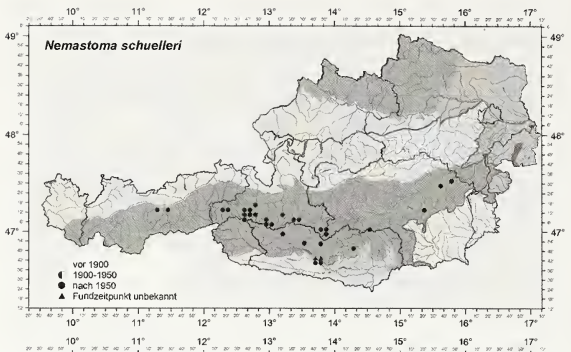
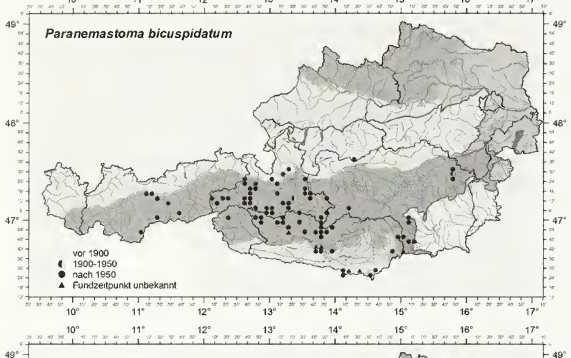
Appendix 1: Distribution patterns for endemic and subendemic harvestmen (Opiliones) in Austria – 11 maps.






Nemastoma bidentatum relictum
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Nemastoma schuelleri
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Paranemastoma bicuspidatum
vor 1900
1900-1950
nach 1950
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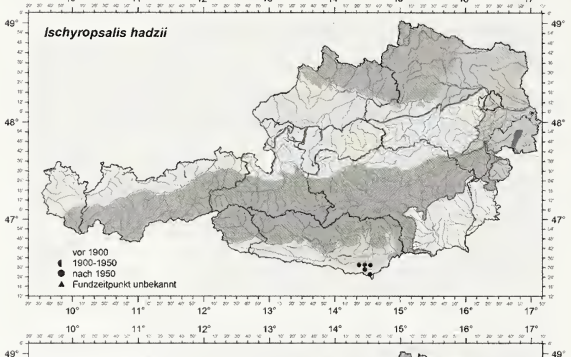
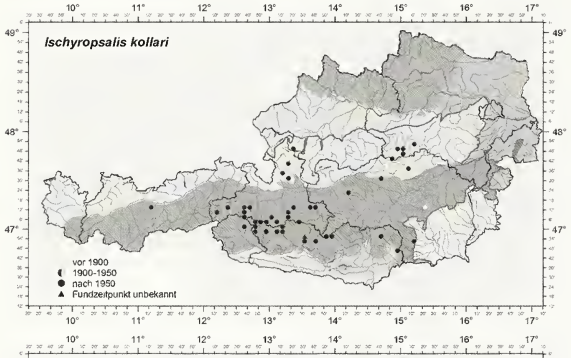

Ischyropsalis hadzii
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Ischyropsalis kollari
vor 1900
1900-1950
nach 1950
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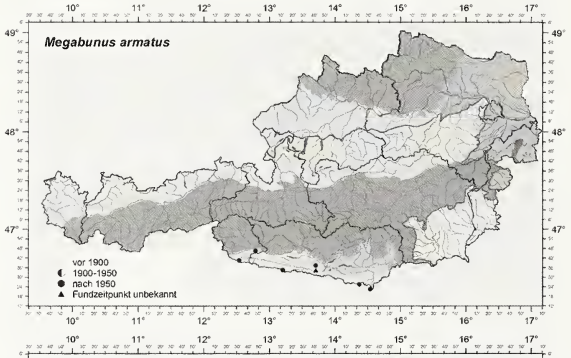
Megabunus armatus
vor 1900
1900-1950
nach 1950
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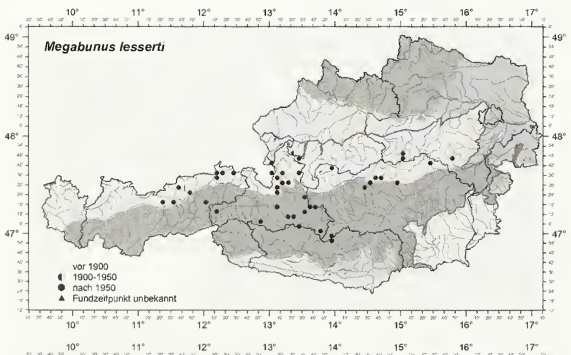
Megabunus lesserti
vor 1900
1900-1950
nach 1950
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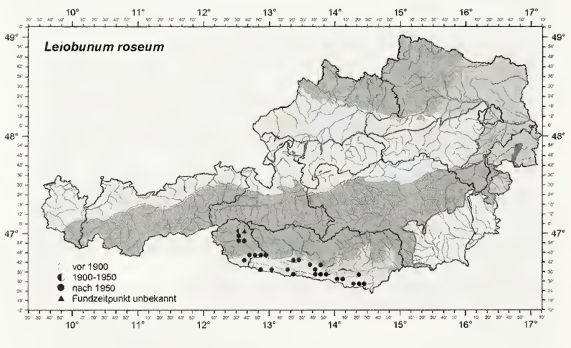
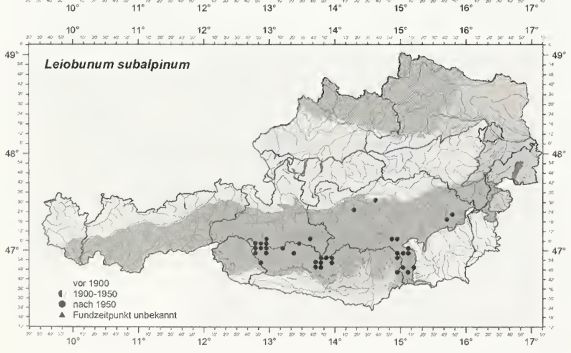

Leiobunum roseum
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Leiobunum subalpinum
vor 1900
1900-1950
nach 1950
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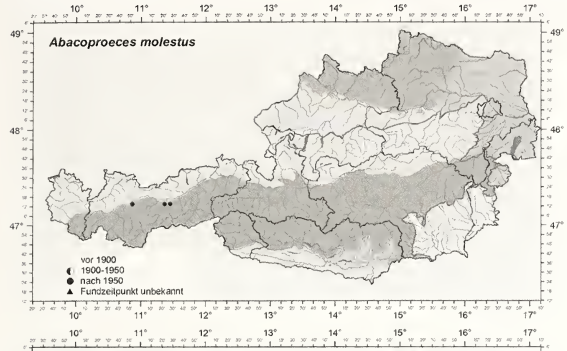
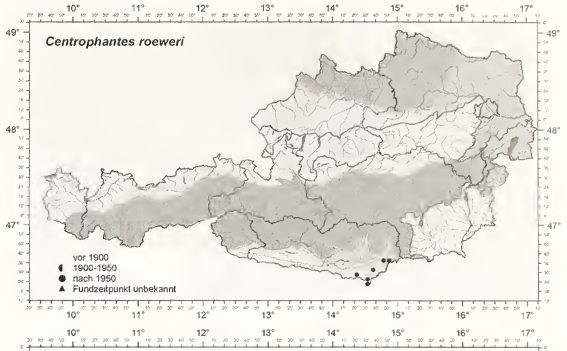
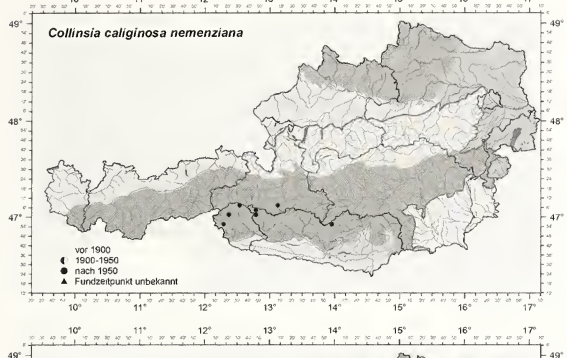
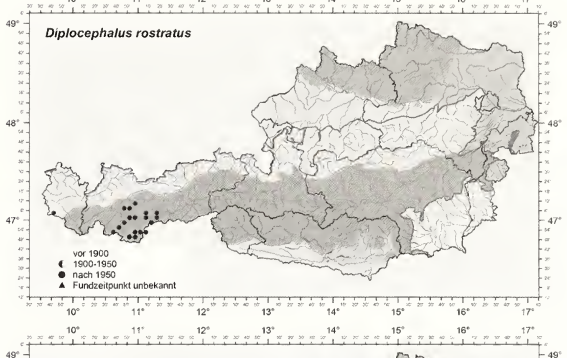
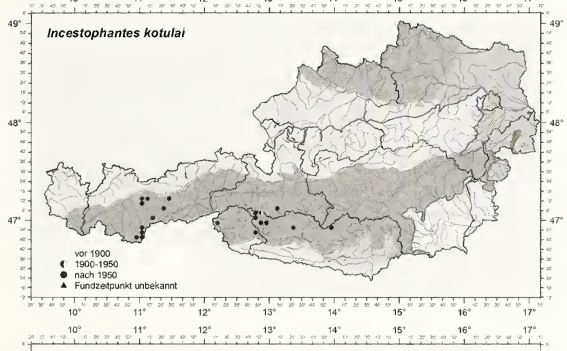
Appendix 2: Distribution patterns for endemic and subendemic spiders (Araneae) in Austria – 46 maps.

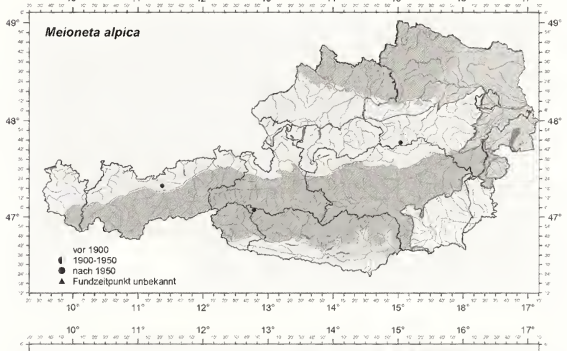


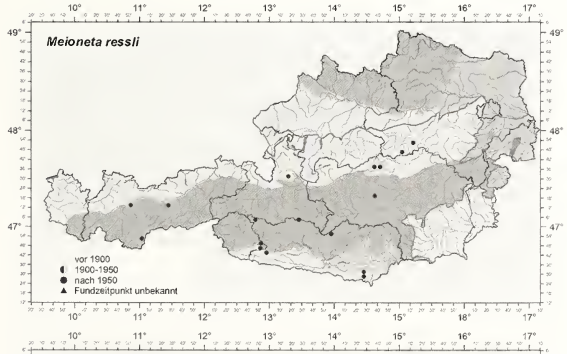


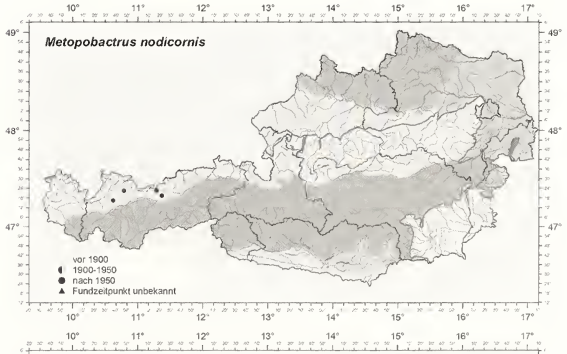


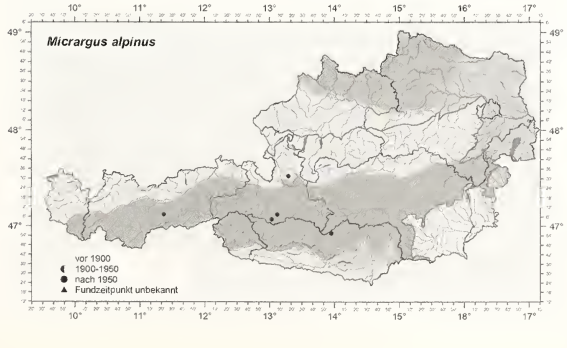


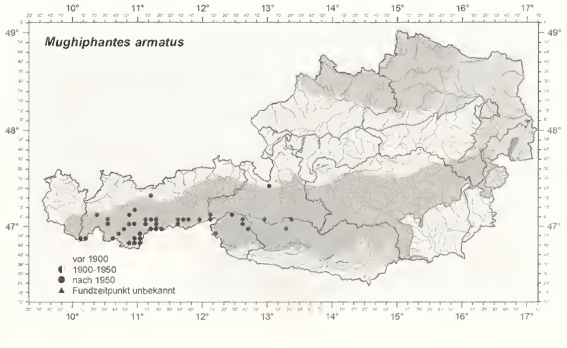


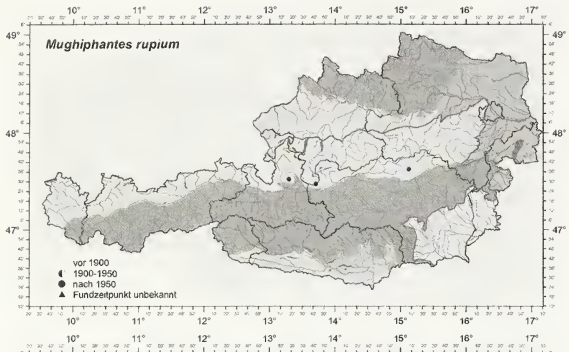


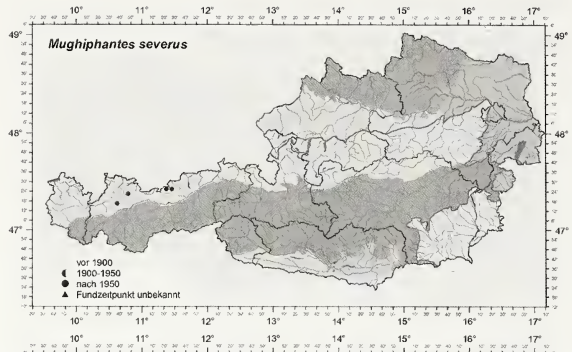


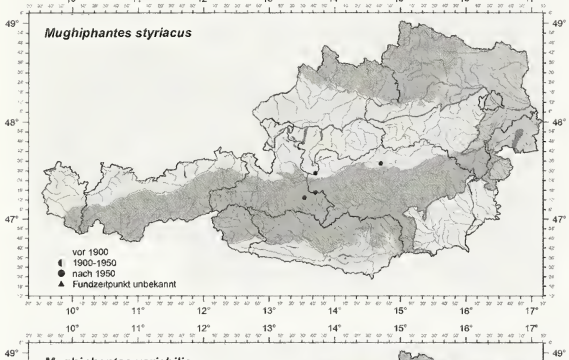







Mughiphantes rupium
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Mughiphantes severus
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Mughiphantes styriacus
vor 1900
1900-1950
nach 1950
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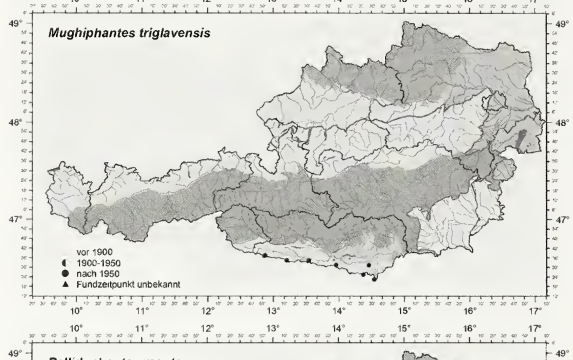
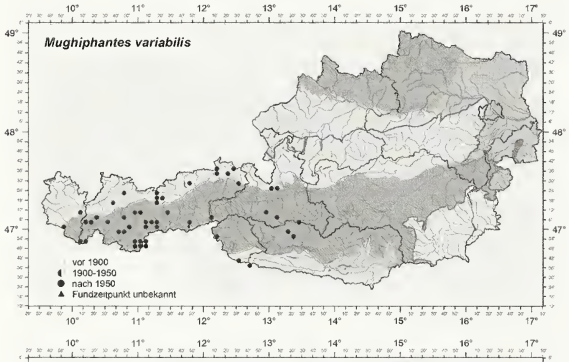
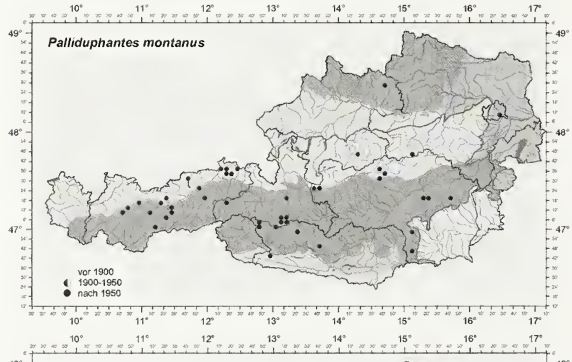
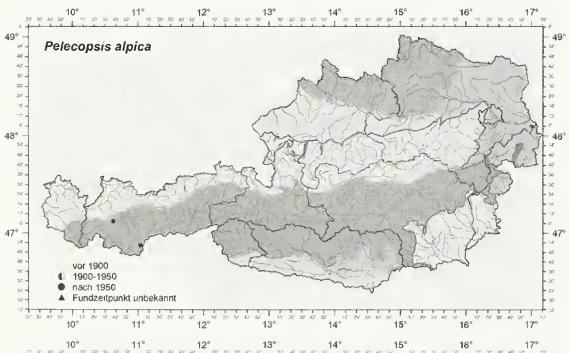
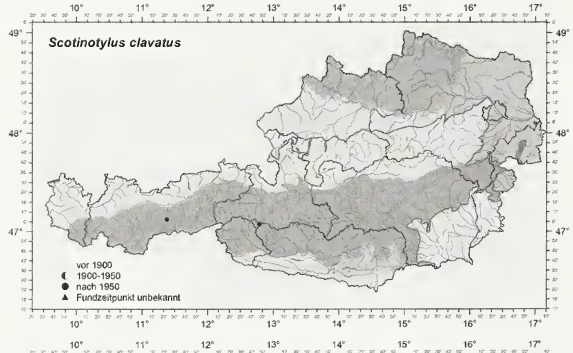
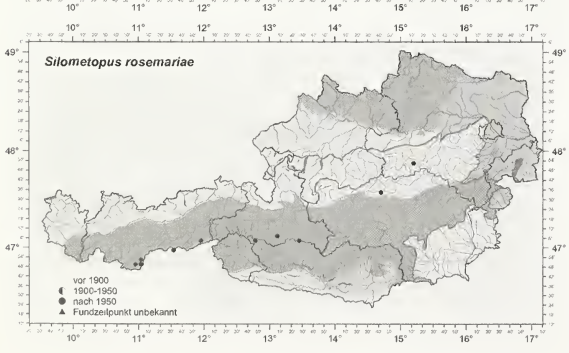

Mughiphantes triglavensis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

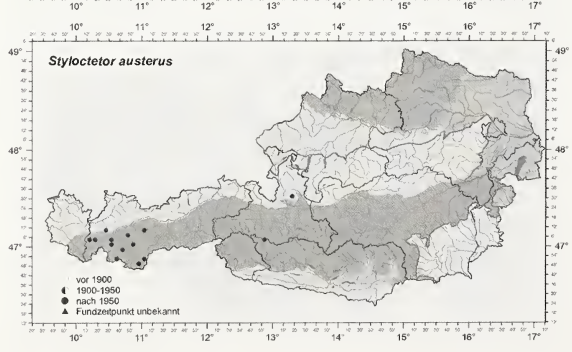

Mughiphantes variabilis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

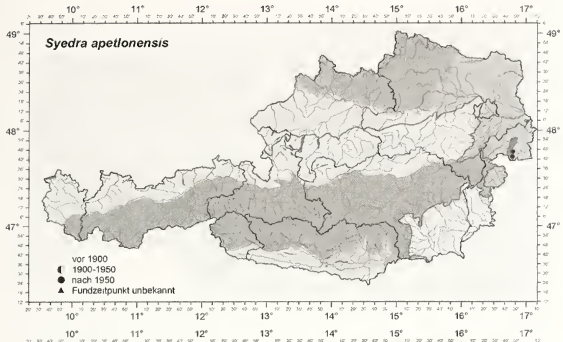

Palliduphantes montanus
vor 1900
1900-1950
nach 1950

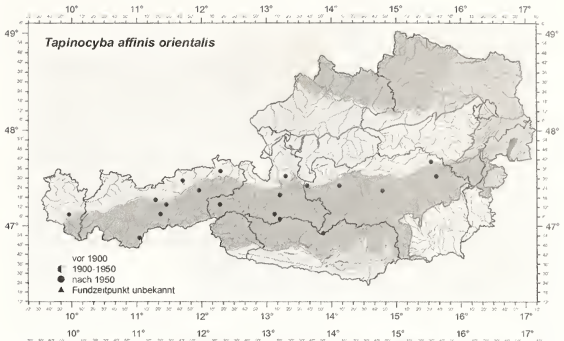

Pelecopsis alpica
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

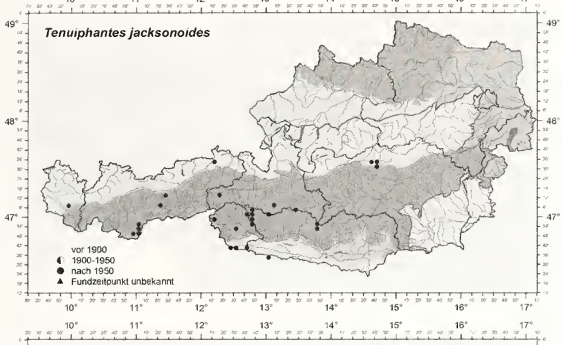

Scotinotylus clavatus
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

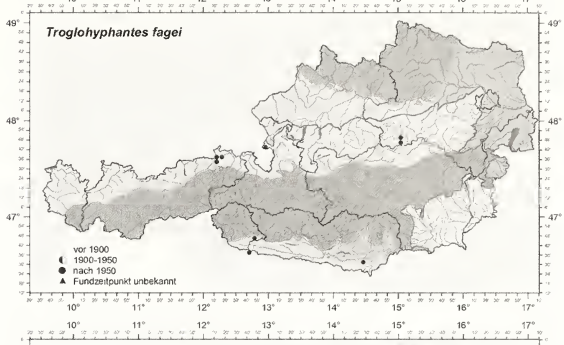

Silometopus rosemariae
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

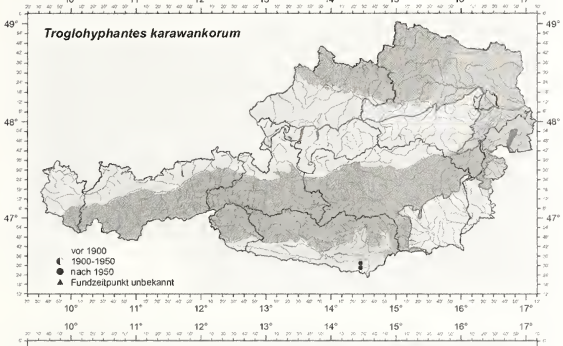

Styloctetor austerus
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

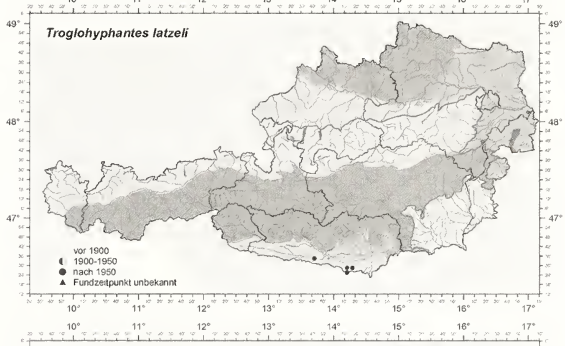

Syedra apetlonensis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

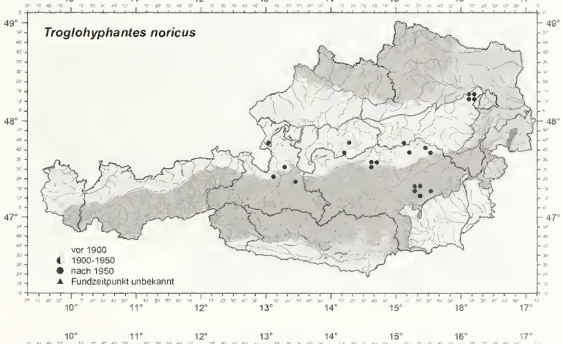

Tapinocyba affinis orientalis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Tenuiphantes jacksonoides
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes fagei
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes karawankorum
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes latzeli
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes noricus
vor 1900
1900-1950
nach 1950
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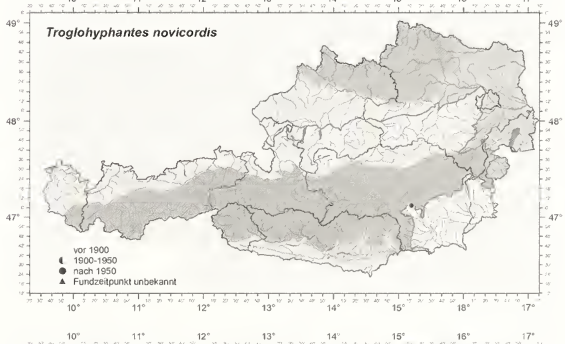
Troglohyphantes novicordis
vor 1900
1900-1950
nach 1950
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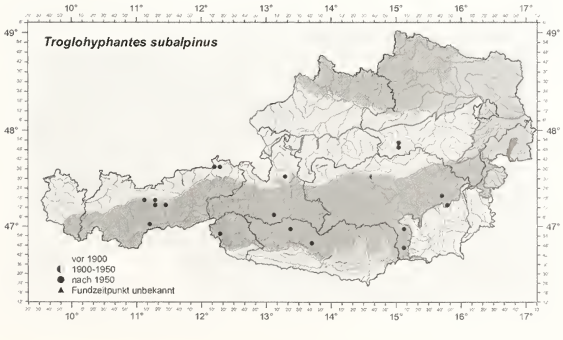
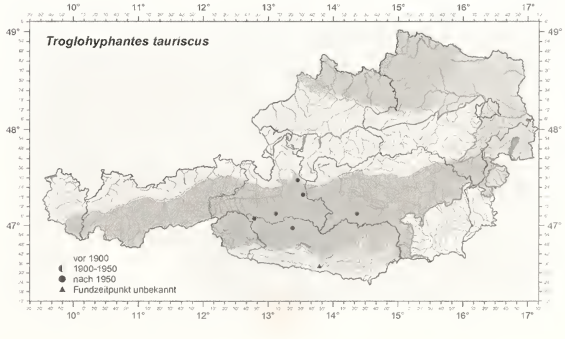
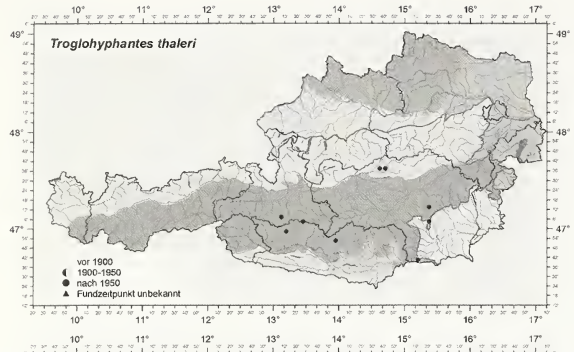

Troglohyphantes subalpinus
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes tauriscus
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Troglohyphantes thaleri
vor 1900
1900-1950
nach 1950
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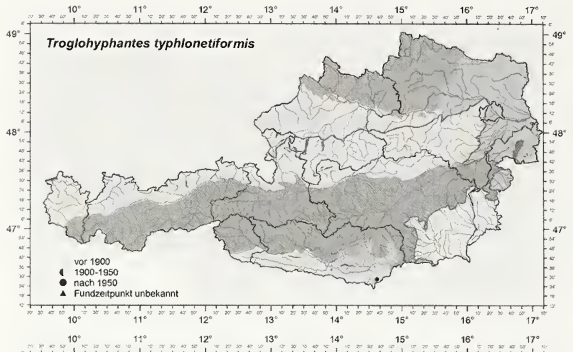
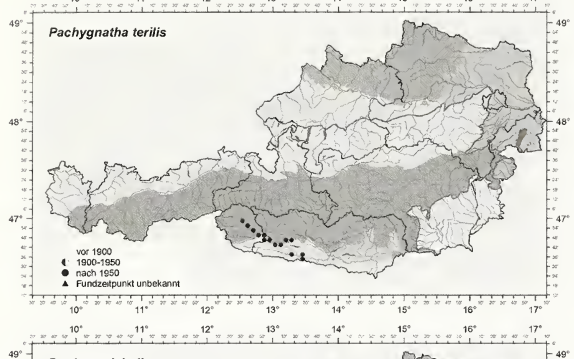
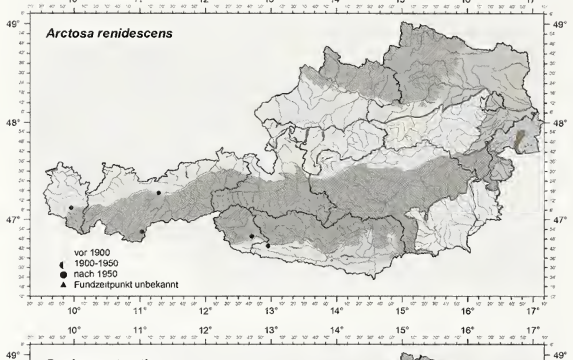
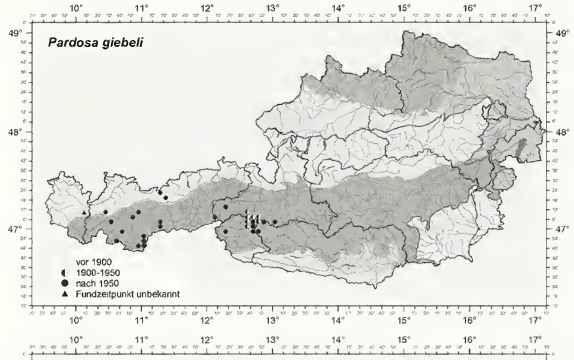

Troglohyphantes typhlonetiformis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Pachygnatha terilis
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt


Arctosa renidescens
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt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vor 1900
1900-1950
nach 1950
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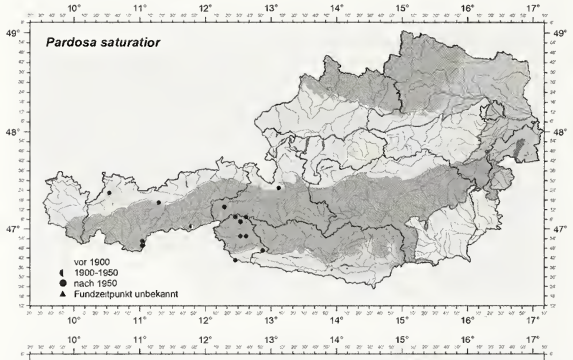
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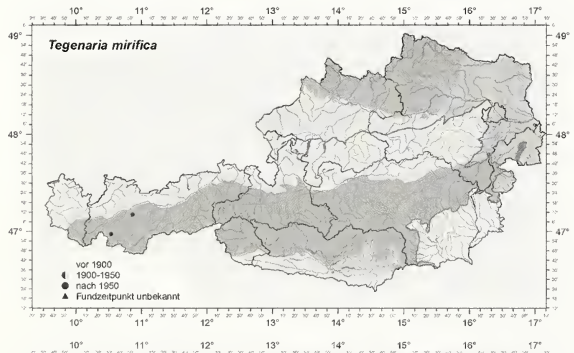
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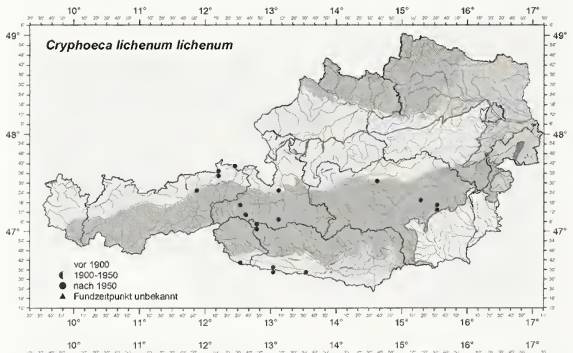
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1900-1950
nach 1950
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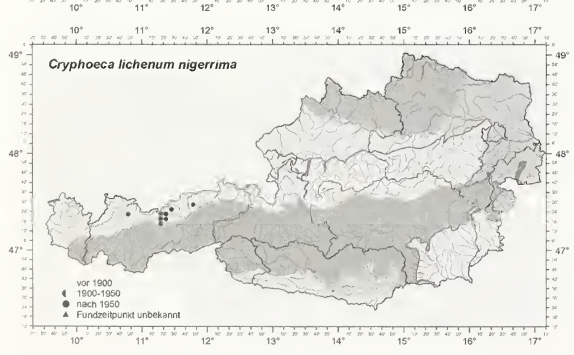
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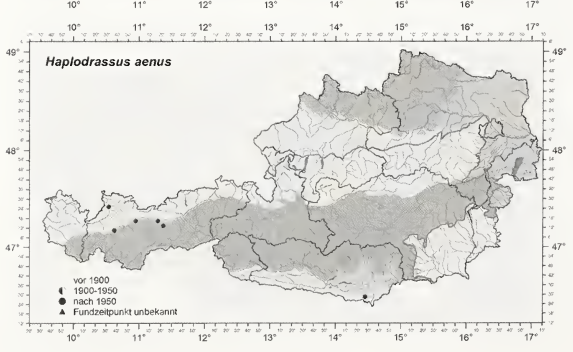
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vor 1900
1900-1950
nach 1950
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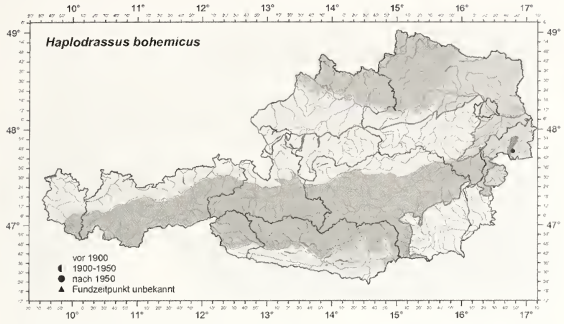
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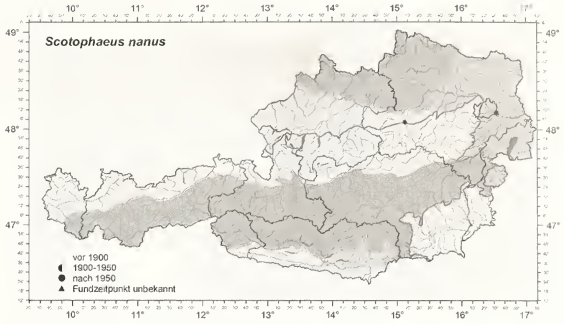
Scotophaeus nanus
vor 1900
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nach 1950
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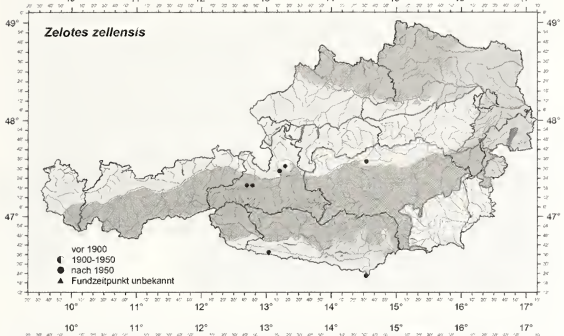
Zelotes zellensis
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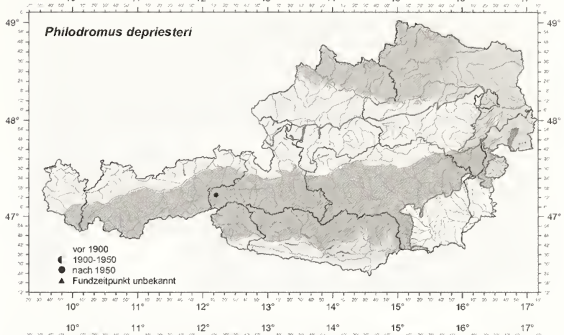
1900-1950
nach 1950
Fundzeitpunkt unbekannt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1900-1950
nach 1950
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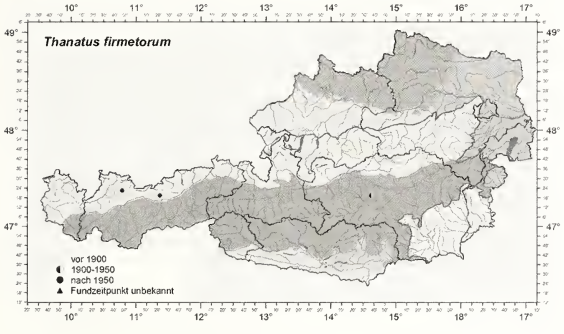
Thanatus firmetorum
vor 1900
1900-1950
nach 1950
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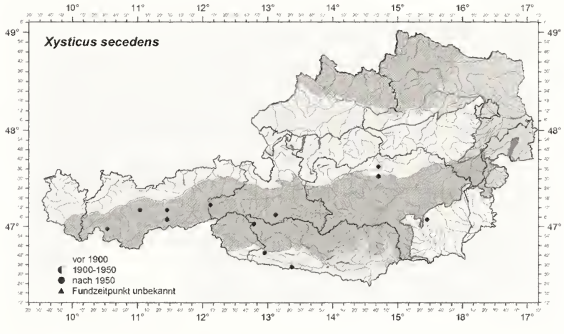
Xysticus secedens
vor 1900
1900-1950
nach 1950
Fundzeitpunkt unbekannt

Ground-living spiders (Araneae) at polluted sites in the Subarctic

Seppo Koponen

doi: 10.5431/aramit4009

Abstract: Spiders were studied around the Pechenganikel smelter combine, Kola Peninsula, north-western Russia. The average spider density was 6-fold greater and the density of Linyphiidae specimens 11.5-fold higher at slightly polluted sites, compared with heavily polluted sites. Altogether, 18 species from 10 families were found at heavily polluted sites, the theridiid *Robertus scoticus* clearly dominating (23.3 % of identifiable specimens), also *Neon reticulatus* (9.6 %), *Thanatus formicinus* (9.6 %) and *Xysticus audax* (8.2 %) were abundant. The most numerous among 58 species found at slightly polluted sites were *Tapinocyba pallens* (18.5 %), *Robertus scoticus* (13.7 %), *Maso sundevalli* (9.5 %) and *Alopecosa aculeata* (8.2 %). The family Linyphiidae dominated at slightly polluted sites, 64 % of species and 60 % of individuals; compared with heavily polluted sites, 23 % and 38 % respectively.

Key words: density, diversity, Kola Peninsula, smelter

In the late 1980's, reports of heavy pollution loads from the Russian smelters in the Kola Peninsula and their possible effect on needle losses among pine in northern Finland prompted active studies on effects of pollution on forest ecosystems in northern Finland, Russia and Norway (see KOZLOV et al. 1993, TIKKANEN & NIEMELÄ 1995).

Spiders, like some other predatory arthropod groups, have been observed at heavily polluted sites near smelters in northern Europe (BENGTSSON & RUDGREN 1984, KONEVA 1993, KOPONEN & NIEMELÄ 1994, KOPONEN & KONEVA 2006). Generally, markedly high concentrations of heavy metals have been found in spiders near pollution sources (BENGTSSON & RUNDGREN 1984, KOPONEN & NIEMELÄ 1995, MAELFAIT & HENDRICKX 1998), and spiders have often been used as indicators in monitoring the effects of pollution (e.g. CLAUSEN 1986). In the present paper, information will be given on spider assemblages near the Pechenganikel smelter complex, in the subarctic Kola Peninsula, NW Russia.

For general data on the nature and degree of pollution in the area, see KOZLOV et al. (1993, 2009) and NORWEGIAN POLLUTION CONTROL AUTHORITY (2002). Spider densities near the Pechenganikel smelter have been briefly dealt with by KONEVA & KOPONEN (1993). For the spider fauna of natural forests in the subarctic and northern boreal taiga zones in Fennoscandia, see e.g. KOPONEN (1977, 1999) and RYBALOV (2003).

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submitted: 17.1.2010, accepted: 17.3.2010; online: 10.1.2011

Figure 1: Pechenganikel (the study area) and Monchegorsk smelters in Kola Peninsula.

Material and Methods

The present study area, the Pechenganikel smelter combine (Nikel and Zapolyarny), ca 69°30'N, 30°20'E, is situated in a subarctic pine forest area, where there are also birch woods, bogs and treeless fells (Fig. 1). The altitude of sites varies between 100 and 200 m asl. The smelter is very close to Norway (only about 10 km from the border) and to Finland (40 km from the border), and the distance to the Arctic Ocean is about 50 km. The yearly mean temperature is about -1°C, and permanent snow cover lasts 6-7 months.

Yearly emission in 1990, just before the spider sampling, was about 250 000 tons SO_2, ca. 200 tons Cu, 300 tons Ni and 10 tons Co (see KOZLOV et al. 2009). This means that sulphur load was the same as in Monchegorsk smelter, central Kola Peninsula, but copper, nickel and cobalt loads were only 10 % of

Table 1: Composition of the spider fauna in the studied heavily (5 sites) and slightly polluted areas (9 sites), Pechenganikel.

	Heavily polluted (H)	Slightly polluted (S)	S/H
Species	18	58	
Species/site	3.6	6.4	1.8
Families	10	13	
Individuals	101	1083	
Ind./m²	20.2	120.3	6.0
range	3-32	71-266	
Linyphiidae ind./m²	7.6	87.7	11.5
% of Linyphiidae (of spec.)	22.2	63.8	2.9
% of Linyphiidae (of ind.)	37.6	59.8	1.6
% of Lycosidae (of ind.)	10.9	11.7	1.1
% of the most dominant species	23.3	18.5	

density was 6-fold greater and the density of Linyphiidae specimens even 11.5-fold at slightly polluted sites. Also species number/site was higher at slightly polluted sites: 1.8-fold. Altogether, 18 and 58 species of spiders were caught in heavily (5 sites) and slightly (9 sites) polluted areas, respectively. Interestingly, as many as 10 families but only 18 species were found at heavily polluted sites, and at slightly polluted sites the material was much more species-rich, but represented no more than 13 families.

that in Monchegorsk. The area of complete damage to forests was 45 km² and severe damage 300 km² around the Pechenganikel complex; in these areas SO_2 concentration was over 80 g/m³, and annual dry sulphur deposition ca 4 g/m² (GYTARSKY et al. 1997, NORWEGIAN POLLUTION CONTROL AUTHORITY 2002).

Spiders were collected at five study sites in heavily polluted areas, 2.5 – 7 km from the smelter, and at nine sites in slightly (or moderately) polluted areas, 6 – 55 km from the smelter.

The average cover of ground and field layer vegetation indicates the degree of pollution: 30 % coverage at heavily and 80 % at slightly polluted sites. Thus heavily polluted sites are more open and because the ground is often black, their microclimatic conditions in summer are more extreme, i.e. they are much drier and warmer than at slightly polluted sites.

Ground- and soil-living spiders were collected, in 1991–92 from 25 x 25 cm squares by hand-sorting. The field work was done by Dr. Galina G. Koneva (Moscow) and identification was by the author. The material consists of ca 620 identifiable spider specimens (of the total 1185 individuals) and is deposited in the Zoological Museum, University of Turku, Finland.

Results

Great differences were found (Table 1) in the density of spiders in heavily and slightly polluted areas, the averages being 20 and 120 ind./m² (ranges 3–32 and 72–266 ind./m²) respectively. The average spider

The theridiid *Robertus scoticus* clearly dominated at the heavily polluted sites (Table 2: 23.3 % of identifiable specimens), and was the second most abundant at the slightly polluted sites (Table 3: 13.5 %). Other abundant species at heavily polluted sites were *Neon reticulatus* (9.6 %), *Thanatus formicinus* (9.6 %), *Xysticus audax* (8.2 %), *Agyneta gulosa* (5.5 %), and *Alopecosa aculeata* (5.5 %). Of these, especially *A.*

Table 2: Total number of spider specimens found at five most polluted and damaged sites (2.5 – 7 km from the smelter), Pechenganikel.

Robertus scoticus	17	23.3 % of identifiable
Neon reticulatus	7	9.6
Thanatus formicinus	7	9.6
Xysticus audax	6	8.2
Agyneta gulosa	4	5.5
Alopecosa aculeata	4	5.5
Haplodrassus sp.	4	5.5
Dictyna uncinata	3	4.1
Evarcha falcata	3	4.1
Heliophanus sp.	3	4.1
Micaria alpina	3	4.1
Scandichrestus tenuis	3	4.1
Xysticus obscurus	3	4.1
Tapinocyba pallens	2	
Pardosa palustris	1	
Tetragnatha sp.	1	
Tibellus maritimus	1	
Walckenaeria antica	1	
Number of species	**18**	
Number of identifiable specimens	**73**	

Table 3: Total number of specimens of the most abundant spiders found at nine slightly polluted sites (6 – 55 km from the smelter), Pechenganikel.

Tapinocyba pallens	101	18.5 % of identifiable
Robertus scoticus	75	13.7
Maso sundevalli	52	9.5
Alopecosa aculeata	45	8.2
Micrargus herbigradus	29	5.3
Hahnia ononidum	26	4.8
Macrargus rufus	18	3.3
Centromerus arcanus	16	2.9
Pardosa hyperborea	15	2.7
Evarcha falcata	12	2.2
Agyneta gulosa	11	2.0
Palliduphantes antroniensis	11	2.0
Xysticus obscurus	11	2.0
Minyriolus pusillus	10	
Microcentria pusilla	7	
Neon reticulatus	7	
Sisicus apertus	7	
Macrargus multesimus	6	
Porrhomma pallidum	6	
Xysticus audax	6	
Cnephalocotes obscurus	5	
Walckenaeria karpinskii	5	
Gnaphosa microps	4	
Micaria alpina	4	
Pardosa palustris	4	
Pocadicnemis pumila	4	
Scotinotylus alpigena	4	
Scandichrestus tenuis	4	
Haplodrassus signifer	3	
Hilaira herniosa	3	
Microneta viaria	3	
Tenuiphantes mengei	3	
Zora nemoralis	3	
Bolyphantes luteolus	2	
Cercidia prominens	2	
Clubiona trivialis	2	
Gnaphosa sticta	2	
Gonatium rubens	2	
Pelecopsis mengei	2	
Robertus lyrifer	2	
Semljicola faustus	2	
Tenuiphantes tenebricola	2	
Thanatus formicinus	2	
Agnyphantes expunctus	1	
Agyneta conigera	1	
Agyneta subtilis	1	
Bolehthyphantes index	1	
Decipiphantes decipiens	1	
Dictyna sp.	1	
Diplocentria bidentata	1	
Gonatium rubellum	1	
Oreonetides vaginatus	1	
Tetragnatha sp.	1	
Tibellus maritimus	1	
Walckenaeria dysderoides	1	
Walckenaeria lepida	1	
Walckenaeria nudipalpis	1	
Zornella cultrigera	1	
Number of species	**58**	
Number of identifiable specimens	**547**	

aculeata and also *Agyneta gulosa* were found in good numbers at slightly polluted sites. Altogether, four linyphiid species (i.e., *Agyneta gulosa, Scandichrestus tenuis, Tapinocyba pallens,* and *Walckenaeria antica*) were found among the total 18 species (22 %) at heavily polluted sites. Only one linyphiid was among the six most abundant spider species (Table 2). The percentage of Lycosidae specimens was about 11 % (Table 1).

The most abundant species at slightly polluted sites (Table 3) were *Tapinocyba pallens* (18.5 %), *Robertus scoticus* (13.7 %), *Maso sundevalli* (9.5 %), *Alopecosa aculeata* (8.2 %), *Micrargus herbigradus* (5.3 %), *Hahnia ononidum* (4.8 %), and *Macrargus rufus* (3.3 %).

The dominant species of the slightly polluted sites, *Tapinocyba pallens*, was found at the heavily polluted sites but only in small numbers. About 64 % of all species and 60 % of specimens at slightly polluted areas belonged to the family Linyphiidae. Three linyphiids were among the six most abundant species. The percentage of Lycosidae was 12 % of all individuals caught (Table 1).

Discussion

Leg deformations or other injuries caused by pollution, could not be found in spiders collected at the polluted sites. Deformations have been observed previously in, e.g., oribatid mites near a smelter (EEVA & PENTTINEN 2009).

The average spider density (about 120 ind./m^2) at slightly polluted sites was of the same magnitude as found previously in natural northern boreal or subarctic forests (e.g. KOPONEN 1977). Also the species composition and the great proportion of Linyphiidae among species and specimens in slightly polluted areas resembled the situation in natural forest habitats. The family Linyphiidae is known to dominate in

the ground layer of northern areas (e.g. KOPONEN 1993).

Proportions of Lycosidae specimens were almost equal and rather low at heavily and slightly polluted sites, i.e. 11 % and 12 %, respectively. In southern Finland, *Xerolycosa* and *Alopecosa* species dominated at the most polluted sites near a smelter (KOPONEN & NIEMELÄ 1994). On the other hand, lycosids were not found in the eroded industrial barren area close to the Monchegorsk smelter, central Kola Peninsula (KOPONEN & KONEVA 2006). However, different collecting methods, pitfall traps in southern Finland and hand-sorting both in Pechenganikel and Monchegorsk, must be borne in mind.

When spiders along a pollution gradient were studied by KOPONEN & KONEVA (2006) near the Monchegorsk smelter complex, *Robertus scoticus* and *Agyneta gulosa* were also found there in the most polluted areas (black, dead barren sites 2.5–5 km from the smelter). In addition to these two species, only *Steatoda phalerata* occurred at the most polluted sites. *S. phalerata* was not found in the Pechenganikel area at all; which may have conditions too harsh for this thermophilous species. Of the present species found at heavily polluted sites, *Micaria alpina, Alopecosa aculeata*, *Evarcha falcata* and *Tapinocyba pallens* were caught in good numbers at rather heavily polluted sites in Monchegorsk (10 km from the smelter). The spider densities near the Monchegorsk smelter were lower than in the present study area (KOPONEN & KONEVA 2006), probably indicating the effect of much greater copper and nickel emissions at Monchegorsk (see Material and Methods).

Emissions of heavy metals and especially sulphur dioxide have decreased greatly since the field work of this paper. According to KOZLOV et al. (2009), the decrease in emissions from 1985 (heavy pollution period) to 2005 was for SO_2 about 70 %, Co 75 %, Cu 20 %, and Ni 15 %. However, pollution in the study area has continued all the time, and emissions at the beginning of this century were still above the critical level for sensitive biota (NORWEGIAN POLLUTION CONTROL AUTHORITY 2002). Thus the environment for the ground-living fauna is nowadays not better than in the early 1990s.

Acknowledgements

I wish to thank Dr. Galina G. Koneva (Moscow) for collecting and sorting the spider material, and Dr. Mikhail V. Kozlov (Turku) for organizing a trip to the Pechenganikel area in 2006.

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Arachnologische Mitteilungen 40: 85-93 Nuremberg, January 2011

Ground spider communities in experimentally disturbed Mediterranean woodland habitats

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doi: 10.5431/aramit4010

Abstract: The protected Mediterranean woodland habitats in Israel are undergoing tree encroachment, resulting in loss of open patches with herbaceous vegetation. We suggested that this process results in a ground spider community dominated by shade-loving species. At three Mediterranean woodland sites located along a rainfall gradient, we examined the effects on the ground-spider community of experimental removal of the woody vegetation in 1000 m^2 plots by cutting and overall plant biomass reduction by grazing and browsing by livestock. Pitfall traps were placed in replicated plots of four treatments (control, cutting, grazing/browsing, and cutting together with grazing/browsing) and in two different habitat patch types (open, woody). ANOVA and multivariate analyses were performed on family abundance by treatment and habitat patch type. Tree-cutting reduced the number of families in plots at two of the three sites. Grazing did not have a significant effect on the number of families or on the ground spider community composition. The spider community of cut-woody patches was more similar to that of open patches than to that of uncut woody patches. Most spider families separated along an axis of open versus woody patches, with woody habitat families predominating at all sites. Families typical of open habitats were positively associated with cut-woody patches as well. The overall effect on ground spider diversity of such manipulations may depend on the scale of habitat changes.

Key words: diversity, family composition, ordination, patchiness, similarity

Patterns of diversity and community structure are the consequence of a large number of factors operating at small and large scales. These effects of different factors may be deduced by investigating the naturally occurring patterns over a range of sites (e.g. OXBROUGH et al. 2005, DE MAS et al. 2009). However, this is a static approach and differences among sites may result from historical as well as current factors. Large-scale habitat manipulation experiments provide an opportunity to examine changes in communities over time at multiple levels of organization and in different groups of organisms (BROWN et al. 2001). Large-scale controlled manipulations will change habitat features in such a way as to provide insight into how specific changes affect communities (SHACHAK et al. 2008). In the present study, we use such an experimental approach to examine effects of a manipulation at the landscape scale on the composition of spider communities at the habitat scale in a Mediterranean ecosystem.

Mediterranean landscapes are patchy, with patches consisting mostly of two habitat types: woody patches that are occupied by shrubs or trees, and contrasting open patches that are devoid of woody plants (NAVEH 1982, GABAY et al. 2008). In protected Mediterranean woodland areas in Israel, the proportion of area covered by woody patches increases along a climatic gradient from south to north with increasing annual precipitation and productivity (KADMON & DANIN 1997). Open patches are mostly covered by herbaceous vegetation that is green in the winter and spring months (January-April) and otherwise dry. Mediterranean woodlands in Israel have been exposed to regimes of grazing and forest cutting for thousands of years (NAVEH & DAN 1973). The combined effect of disturbance from intensive grazing and browsing by livestock, and removal of woody vegetation for firewood, has maintained the mosaic of open and woody patches in the Mediterranean landscape. With the establishment of nature reserves in the Mediterranean region of Israel, grazing and tree-cutting were largely eliminated; consequently the woodland became more closed and with reduced cover of grasses and annual plants (PEREVOLOTSKY 2006). Such changes could have positive and negative effects on biodiversity of different groups of organisms owing to a number of different processes that may act in different ways. For example, the increased structural diversity of trees may create more niches for arboreal arthropods, while increased shade may lower annual plant productivity and reduce arthropod abundance in the understory.

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submitted: 19.1.2010, accepted: 24.3.2010; online: 10.1.2011

The effect of encroachment of the woodland and subsequent re-opening by cutting and grazing on the diversity of a range of organisms was the aim of a multi-year investigation of biological diversity in three Mediterranean woodland sites along a precipitation gradient in Israel (SHACHAK et al. 2008). In this study, we tracked the changes in community composition of ground-active spiders in woody and open patches following two large-scale manipulations of the landscape: 1) tree cutting and removal of the woody vegetation canopy and 2) grazing and browsing. The structure of the habitat is well-known to influence habitat selection by spiders (e.g., UETZ 1991, LANGELLOTTO & DENNO 2004, MALLIS & HURD 2005) and thus was expected to affect community composition following the manipulation. We report on the changes following the manipulations, concentrating on effects of cutting and woody vegetation removal on the spider community found in the two habitat patch types. Our working hypothesis was that creating large open areas in the landscape by removal of woody canopy will change the spider community composition from predominantly shade-loving taxa to a community dominated by taxa typical of open habitats, and that this change will be accompanied by a loss of shade-loving taxa.

Methods

Research sites and experimental design

The study was conducted in three Long-term Ecological Research sites in the Mediterranean region of Israel, listed from south to north: Adulam – in the Adulam Nature Reserve near Bet Guvrin (31°40' N, 34°50' E, 200 m elevation, ca. 400 mm annual rainfall), Ramat Hanadiv – in the southern Carmel mountains near Zichron Ya'acov (32°30' N, 34°55' E, 120 m elevation, ca. 600 mm annual rainfall), and Meron – on the slopes of Mt. Meron in the Upper Galilee (33°15' N, 35°25' E, 850 m elevation, ca. 900 mm annual rainfall). All of these sites have a canopy of small trees (3-5 m height) and woody shrubs, dominated by *Quercus calliprinos* and *Pistacia palaestina* at Meron (ZOHARY 1973), *Phillyrea media*, *Pistacia lentiscus* and *Sarcopoterium spinosum* at Ramat Hanadiv (BAR MASSADA et al. 2008) and *Phillyrea media* and *Pistacia lentiscus* at Adulam (MILMAN 2007).

At each site, 5-6 blocks were marked and within each block we established four plots of 1000 m^2 each. Each plot within a block received a different treatment, such that the treatments were replicated across the blocks. The treatments were: 1) control (no manipulation of the habitat), 2) grazing and browsing, 3) cutting and removal of the woody vegetation from the plot, and 4) cutting and woody plant removal together with grazing and browsing. Grazing and browsing by livestock was introduced into the plots in the late spring (May-June) after the arthropod sampling. Livestock used were typical of the region, sheep at Adulam, goats at Ramat Hanadiv and cows at Meron. Grazing pressure was moderate and typical of the area, with the exception of Ramat Hanadiv where grazing was more intensive. Cutting and removal of the woody vegetation was done in the late autumn. The trees and woody shrubs were cut at the base and the above-ground parts were removed from the plot. Each site was cut twice during the four-year study, once in the first year and repeated in the second year, with the exception of Adulam, where cutting was repeated after a 2-year interval.

We measured ground spider activity-density using pitfall traps, which were set for 5 days in the late spring of 2006 (April-May), the season in the Mediterranean ecosystem when many plants are flowering and there is new growth of herbaceous vegetation. Flowering in spring begins in the south and progresses northward, such that the peak of flowering at the northernmost site (Meron) is about one month later than at the southern site (Adulam). Pitfall trapping was timed at each site to the local flowering period. At each site, dry pitfall traps consisting of two plastic cups (10 cm diameter at the top x 10 cm height) placed one inside the other were dug into the ground such that the rim was flush with the surface. In each plot there were 18 traps: three traps in each of three patches beneath trees or woody shrubs and, similarly, three traps in each of three open patches with herbaceous vegetation cover. In cut plots, traps were placed in former woody patches; these were easily distinguished by the remaining base of the tree or shrub and an area of leaf litter surrounding it. The samples from the three traps in each patch were combined. Thus, the samples in all analyses represent three replicates per patch type per plot. The traps were positioned and kept closed 1-2 weeks before the trapping began to allow the ground to settle around the traps. The traps were checked every morning for 5 days and each day all spiders were collected and transferred to 70 % alcohol for later identification.

All spiders were identified to family level (individuals of unknown family were removed from the data set), and for some families adults were identified to species. The analyses below were performed at the

family level in order to take advantage of the full data set. Classification by family is somewhat arbitrary, as species may be shifted from one family to another. Nevertheless, we justify this approach here because 1) species identification was possible for only some of the families, 2) juveniles constituted 16-40 % of the individuals and could not be reliably identified to species, and 3) creating morpho-species, especially with large numbers of juveniles, would artificially augment the number of species. Species in a family often belong to a single foraging guild and thus analysis by family can provide an indication of composition in relation to the diversity of habitat use and foraging strategies. Finally, we are cautious about inferring species-level processes from those observed at the family level. CARDOSO et al. (2004), for example, showed a significant correlation between numbers of species and families at sites in Portugal, but nonetheless found that species richness could not be inferred from family richness.

Statistical analysis

Factorial ANOVA was performed on the total number of families at each site, with grazing and tree removal as factors and plots as sample replicates. The effect of the different blocks was not significant in any of the analyses and thus this was not entered as a factor.

In order to test for differences in the spider community composition we used multivariate analyses. The analyses were performed on the matrix of family abundance (fourth-root transformed) with plots as the sample replicates and block as a covariable. The environmental variables were the treatments (control, grazing, cutting, cutting and grazing combined) and habitat patch type (open and woody patches).

Analysis of similarity (ANOSIM) was performed on a Bray-Curtis dissimilarity matrix of family abundance with Primer V5.2.2 (CLARKE & GORLEY 2006). ANOSIM was used first to compare family composition in plots of the different treatments (cutting, grazing) and then to compare between specific a priori combinations of treatment and habitat patch type.

To further explore the relationship between the spider family abundance and environmental variables of treatments and patch types we performed constrained ordinations. Detrended correspondence analysis (DCA) was performed to determine which ordination method to use. DCA showed that the length of the gradient was below 3 and therefore the axes were relatively short, implying that the response curves of the family scores were linear. Therefore, principal components analysis (PCA) and redundancy analysis (RDA) are appropriate for these data. We used CANOCO software version 4.53 (TER BRAAK & ŠMILAUER 2004). The points in the two-dimensional PCA graphs represent sample scores of patch types per plot for the first two axes. Thus, the number of samples is equal to the number of plots in which the patch type appeared. In the PCA graphs, the closer the points are to each other, the more similar they are in their family composition.

Redundancy analysis (RDA), also performed in CANOCO (TER BRAAK & ŠMILAUER 2004), was used to determine the environmental variables (treatments and patch type) that best explain the family composition and to determine which families correlate best with the different treatments and patch types. RDA is a form of direct ordination in which axes are constrained by environmental variables and like PCA, it is based on linear correlation responses of the family scores curves (LEPŠ & ŠMILAUER 2003). We used reciprocal averaging of family abundances and site scores (representing the treatment and patch type variables) and manual forward selection with 499 Monte-Carlo permutations, to choose the set of environmental variables to include in the model, selecting only the significant variables. In order to compare among the three sites, we limited the RDA to the 10 most abundant families in each site (11 in Meron, due to a tie between the abundances; see Table 1). These families represent about 90 % of the total abundance in each site.

Finally, we quantified the contribution of the most abundant families to the differences in family composition between treatment and habitat patch type combinations, using the same Bray-Curtis dissimilarity matrix from the ANOSIM (see above). A similarity percentage analysis (SIMPER) was performed in PRIMER (v5.2.2) to calculate the average Bray-Curtis dissimilarity for each family, which is expressed as the average contribution of the family to the overall dissimilarity between pairs of treatment and patch-type combinations.

Results

Sample sizes were small (Table 1), reflecting the relatively low productivity of a seasonal, semi-arid landscape and the short sampling period. The dominant families in all three sites were ground spiders (Gnaphosidae), jumping spiders (Salticidae), wolf spiders (Lycosidae) and ant-eating spiders (Zodariidae). These four families together constituted 78 %, 80 %

Table 1: Total numbers of individuals of the different families collected by pitfall trapping in Mediterranean woodland habitats at three sites in Israel (listed from south to north according to increasing rainfall). The abundances of the ten families used at each site (11 at Meron) for RDA are shown in bold.

Family	Adulam	Ramat Hanadiv	Meron
Agelenidae	**13**	**42**	**10**
Araneidae	4	6	3
Cithaeronidae			2
Clubionidae		3	7
Corinnidae		4	3
Dictynidae		1	1
Dysderidae	**13**	**25**	**40**
Eresidae	2		1
Filistatidae	2	**16**	3
Gnaphosidae	**187**	**190**	**254**
Hahniide	1		**1**
Hersiliidae	**7**		4
Linyphiidae	**29**	**25**	**54**
Liocranidae	2		3
Lycosidae	**145**	**307**	**118**
Miturgidae	4	1	**22**
Nemesiidae		1	
Oecobiidae	**20**		2
Oonopidae	4		1
Oxyopidae	3		2
Palpimanidae	2		2
Philodromidae	6		5
Pholcidae		3	
Pisauridae	4	2	6
Salticidae	**124**	**66**	**91**
Sicariidae	2	1	
Scytodidae	4	**14**	**13**
Segestriidae			2
Theraphosidae	1		
Theridiidae	6	**10**	**14**
Thomisidae	**23**	3	**10**
Zodariidae	**92**	**65**	**134**
Zoridae		1	
Totals	700	786	808

and 74 % of the total abundance in Adulam, Ramat Hanadiv and Meron respectively.

Tree cutting and removal reduced the number of families in Adulam ($F_{1,20}$=13.67, p=0.0014) and in Meron ($F_{1,16}$=26.45, p=0.006), but not in Ramat Hanadiv ($F_{1,16}$=5.0, p>0.5). The effect of grazing and the interaction between grazing and cutting were not significant at any of the sites (Fig. 1). The full ANOVA models (cutting, grazing and the interaction between them) explained 41 % of the variance in number of families in Adulam ($F_{1,20}$=4.63, p=0.012) and 38.5 % in Meron ($F_{1,16}$=3.34, p=0.046), but only 17 % in Ramat Hanadiv ($F_{1,16}$= 1.1, ns).

Analysis of similarity (ANOSIM) based on Bray-Curtis dissimilarity indices showed that family composition differed significantly between cut and uncut plots at all sites (Adulam, global R=0.09, p<0.005; Ramat Handiv, global R=0.06, p=0.051; Meron, global R=0.08, p<0.05) while grazing had no significant effect. When we segregated the cutting treatment according to open and woody patch types, ANOSIM showed that open patches did not differ from one another in family composition, regardless of cutting treatment (Table 2). As cut and uncut open patches did not differ from one another, for the principal components analysis we segregated the samples into three groups: open patches (cut and uncut combined), uncut-woody and cut-woody patches.

In the principal components analysis (PCA) there was no segregation along the first four axes according to grazing, and thus grazing is not shown in the PCA graphs (Fig. 2A, 2C, 2E; see RDA results below). The first principal components axis accounted for 27 % of the spider family variance at Adulam, 34 % at Ramat Hanadiv and 38 % at Meron (Appendix). In Adulam (Fig. 2A) and Meron (Fig. 2E), the first axis separated the samples from woody and open patches, with the cut-woody samples falling closer to the open patches. At these two sites, the variance in the second axis (12 % and 10 %, respectively) was not clearly associated with any treatment or patch-type gradient in the samples. At Ramat Hanadiv, the separation of woody and open samples was along the second axis, which accounted for 16 % of the variance (Fig. 2C). As in Adulam and Meron, the cut-woody samples were closer to the open samples, and indeed, intermixed with them along the second axis. The first axis could not be attributed to either cutting or to the patch type. Adding the grazing treatment did not show a clear pattern along this axis and thus, the first axis represents variation from other unmeasured factors.

In the redundancy analysis (RDA), the first two axes were correlated with the environmental variables of treatment and patch type (Figs. 2B, 2D, 2F; correlation coefficients: Adulam: 0.75 and 0.49 for axes 1 and 2 respectively, Ramat Hanadiv: 0.74 and 0.31, Meron: 0.78 and 0.62). However, the total variance in family composition explained by

Table 2: Analysis of similarity (ANOSIM) tables showing R (similarity index) for the comparison between pairs of treatment and patch type combinations at the three sites. The comparisons are arranged in decreasing order of R values. A high index of similarity ($p<0.05$; shown in italics) indicates that there was a significant difference in family composition between the two treatment-habitat types. Habitat patches in plots that were not cut are noted as 'woody' or 'open', while those in cut plots are noted as 'cut-woody' and 'cut-open'.

A. Adulam

Treatment -patch type	R	Significance
cut-open vs. woody	*0.474*	*0.001*
cut-woody vs. woody	*0.397*	*0.001*
open vs. woody	*0.391*	*0.001*
cut-open vs. cut-woody	*0.098*	*0.03*
cut-open vs. open	0.031	0.2
cut-woody vs. open	-0.034	0.8

B. Ramat Hanadiv

Treatment -patch type	R	Significance
open vs. woody	*0.382*	*0.001*
cut-open vs. woody	*0.31*	*0.001*
cut-woody vs. woody	*0.293*	*0.001*
cut-woody vs. open	0.006	0.4
cut-open vs. open	-0.04	0.7
cut-open vs. cut-woody	-0.06	0.85

C. Meron

Treatment -patch type	R	Significance
open vs. woody	*0.7*	*0.001*
cut-open vs. woody	*0.564*	*0.001*
cut-woody vs. woody	*0.386*	*0.001*
cut-woody vs. open	*0.141*	*0.01*
cut-open vs. cut-woody	0.005	0.4
cut-open vs. open	-0.014	0.5

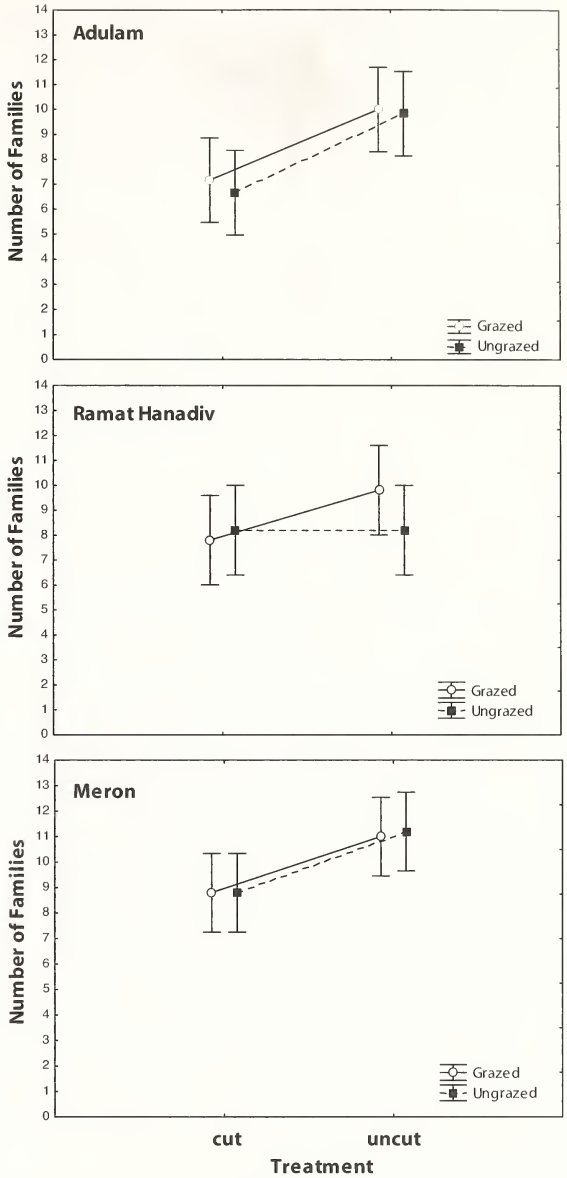
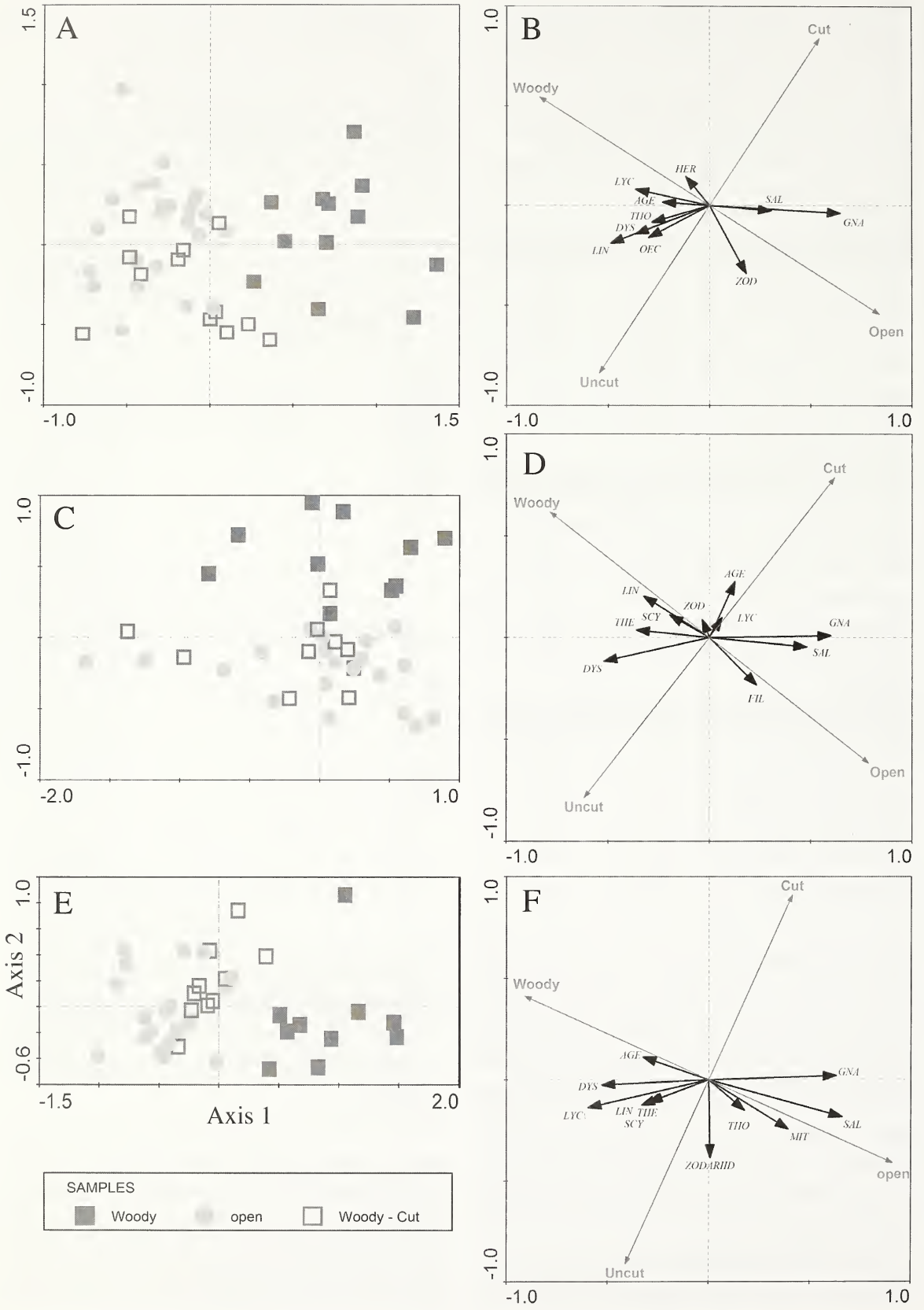


Figure 1: Mean and 95 % CI of the number of families in plots under two landscape manipulations, cutting and grazing, at three Mediterranean woodland sites (from south to north): Adulam (31°40′ N, 34°50′ E, 200 m elevation, c. 400 mm annual rainfall), Ramat Hanadiv (32°30′ N, 34°55′ E, 120 m elevation, c. 600 mm annual rainfall) and Mt. Meron (32°00′ N, 35° 20′E, 900 m elevation, c. 800 mm annual rainfall).

treatment and patch type was low in all three sites (Adulam: 22 %, Ramat Hanadiv: 13 %, Meron: 29 %). Grazing was not a significant variable in any of the sites ($p>0.5$). Both patch type and cutting were significant in Adulam (patch type: $F=6.71$, $p=0.002$; cutting: $F=3.84$, $p=0.002$) and in Meron (patch type: $F=11.21$, $p=0.002$; cutting: $F=3.77$, $p=0.004$). In Ramat Hanadiv patch type was the only significant explanatory variable ($F=2.62$, $p=0.036$); cutting was not significant ($F=1.94$, $p=0.096$), but was included in the analysis as it appears to influence the distribution of some families.

Most of the spider families at the three sites were segregated along the axis of patch type, showing an affinity either to woody patches or to open patches. At Adulam and Ramat Hanadiv, the two southern sites, there were more families associated with woody patches than with open patches (Figs. 2B and 2D, respectively). Families with strong woody-patch affinity (indicated by the length of the arrows) included


A
1.5
-1.0
-1.0
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Cut
Woody
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Open
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1.0
SAMPLES
Woody
open
Woody - Cut

one of the four dominant families, namely the wolf spiders (Lycosidae), as well as sheetweb spiders (Linyphiidae), cobweb spiders (Theridiidae, mainly juveniles of *Crustulina*, *Enoplognatha* and *Euryopis*), and woodlouse hunters (Dysderidae, mainly unidentified species of *Harpactea*). The families associated with the open, herbaceous patches were the remaining three numerically dominant families: the ground spiders (Gnaphosidae, mainly *Pterotricha levantina* Levy, 1995 and *Zelotes scrutatus* (O. P.-Cambridge, 1872) at Meron and Adulam and *Pterotricha cambridgei* (L. Koch, 1872) and *Z. scrutatus* at Ramat Hanadiv), jumping spiders (Salticidae, unidentified species of *Aelurillus* at all sites) and ant-eating spiders (Zodariidae, e.g., *Ranops expers* (O. P.-Cambridge, 1876) and *Zodarion lutipes* (O. P.-Cambridge, 1872) at Meron, *Palaestina expolita* O. P.-Cambridge, 1872 and *Z. lutipes* at Ramat Hanadiv and *Zodarion judaeorum* Levy, 1992 at Adulam). Cutting had a positive influence on funnel-web spiders (Agelenidae, mainly juveniles of *Agelena* and *Maimuna*) and wolf spiders (Lycosidae) at Ramat Hanadiv (Fig. 1D).

Analysis of similarity (ANOSIM) results (Table 2) showed that there were significant differences in family composition between cut-woody patches and woody patches (uncut) at all sites. We conducted a percentage similarity analysis (SIMPER) of family dissimilarity between these two patch types in order to determine which families contributed most to this difference. The results support the segregation of families along the axis of cut-woody versus woody patches as suggested in the RDA. Among the families that contributed the most to the community dissimilarity between these two habitats at Adulam and Meron were Gnaphosidae and Salticidae (together, 36 % and 21 % contribution to dissimilarity at Adulam and Meron, respectively), with higher average abundance of both families in cut-woody patches and Linyphiidae (12.5 % and 11 % contribution, respectively) found only in woody patches. At Ramat Hanadiv, Lycosidae and Gnaphosidae together contributed 49 % of the dissimilarity between cut and uncut woody patches and both had higher average abundance in cut-woody patches.

Figure 2: Multivariate analyses of ground spider families at three sites Adulam (A, B), Ramat Hanadiv (C, D) and Meron (E, F). Figures A, C, and E are show the spider family composition per plot along the first (x) and second (y) principal component axes, coded by patch type (woody, open and cut-woody). Figures B, D, and F show plots of the spider families along the first two RDA axes representing the environmental variables of habitat type (axis 1, woody vs. open) and cutting (axis 2, cut vs. uncut). The spider family codes are: AGE=Agelenidae, DYS=Dysderidae, GNA=Gnaphosidae, HER=Hersiliidae, LIN=Linyphiidae, LYC=Lycosidae, MIT=Miturgidae, OEC=Oecobiidae, SAL=Salticidae, SCY=Scytodidae, THE=Theridiidae, THO=Thomisidae, ZOD=Zodariidae

Discussion

At two of the three sites, plots where trees had been cut and removed (with or without grazing) had fewer spider families on average than did control plots. The ground spider community of cut woody patches differed significantly from that of uncut woody patches and was more similar to that of open patches. Grazing had no significant effect on family richness, nor did it influence the family composition at any of the sites. Intensive grazing and browsing by goats at Ramat Hanadiv reduced the cover of woody vegetation (BAR MASSADA et al. 2008), and yet we found no effect on spider family composition in our analysis. Grazing alone also had little effect on the species richness of herbaceous plants at all three sites (AGRA & NE'EMAN 2009; Y. Lubin, G. Ne'eman & A. Perevolotsky unpubl.). There may be several reasons for the lack of a strong grazing effect. First, the Mediterranean flora and fauna has a long history of grazing and organisms are well-adapted to it (NOY-MEIR et al. 1989, WARD 2005); second, grazing may have been insufficient in duration and intensity to produce a change; and third, the sampling of herbaceous vegetation and of spiders took place several months after the livestock were removed from the plots and there may have been sufficient time for the new annual vegetation to emerge following winter rains and for spiders to re-colonise following the disturbance.

At all sites, cutting and removal of the woody vegetation had a marked effect on the spider family composition at the patch level. Analysis of similarity (ANOSIM) gave low, but significant values of R for the difference between cut and uncut plots. The reason for the low global R values is that the open patches in both cut and uncut plots were similar in family composition, reducing the overall strength of the difference between the two treatments.

The PCA diagrams show that the spiders from former woody patches (cut-woody) were more similar in family composition to those from open patches than to those from uncut woody patches. Thus, community composition shifted from families typically found beneath trees and shrubs toward families typical of open patches with herbaceous vegetation. The

shift was not complete, however, as some cut-woody samples overlapped with the woody samples at all three sites, and there were significant differences in family composition between cut-woody and open habitats at two of the three sites. One reason for the incomplete shift may be that the cut trees re-sprout rapidly following cutting and at the time of sampling most cut trees had new growth to a height of 0.3-1 m, thus providing conditions that may allow shade-loving species to persist or to recolonise. Another option is that, owing to modification of soil characteristics around woody plants (SEGOLI et al. 2008), the litter and soil moisture conditions surrounding the cut tree change only slowly and thus spiders still perceive this habitat as a woody patch.

The distinct family preferences for either woody or open patches are seen in the RDA, as this was the main axis of separation at all three sites. Most families were associated with the tree habitat, an association possibly related to a more favorable microclimate and higher prey abundance. Gnaphosids and salticids were notable exceptions being clearly associated with open patches. Most of the gnaphosid species at these sites are nocturnal (personal observation), while the jumping spiders are all diurnal, which suggests that these two taxa temporally partition the terrestrial niche of open, herbaceous vegetation patches.

Differences in family composition between cut and uncut plots (ANOSIM) largely reflect differences between cut-woody patches and woody (uncut) patches. In the percentage similarity analysis (SIMPER), families that showed strong associations with either open or woody patches in the RDA also contributed the most to the dissimilarity between the cut-woody and woody patches. This again supports the view that open habitat species benefitted from tree cutting. Two families in particular, Agelenidae and Lycosidae, showed an association with cutting at Ramat Hanadiv (RDA) and also contributed the most to the dissimilarity between cut-woody and woody patches at this site (SIMPER). The funnelweb spiders (Agelenidae) at Ramat Hanadiv mostly belonged to a single species, *Agelescape livida* (Simon, 1875). These spiders construct their webs on shrubs and were able to take advantage of an abundance of websites on the regenerating trees (personal observation). A large proportion of agelenids and lycosids trapped at Ramat Hanadiv were juveniles (90 % and 77 %, respectively). Juvenile lycosids and agelenids are highly mobile (e.g., WALKER et al. 1999) and young individuals searching for suitable sites may have moved preferentially into the newly accessible cut-woody patches. At the other two sites, both of these families were associated with the woody habitat. However, overall there were lower proportions of juveniles at Adulam (20 %) and Meron (16 %) than at Ramat Hanadiv (42 %), and in particular, the proportion of juvenile lycosids was lower at these two sites (39 % and 19 %, respectively) than at Ramat Hanadiv. Thus the shift from woody patches into the cut woody patches at Ramat Hanadiv may have been a consequence of the preponderance of mobile juveniles in these two families.

In conclusion, opening the woodland by tree-cutting had a small, but significant effect on family richness, and a pronounced effect on spider family composition. In general, there was a shift of family composition from predominately woody habitat taxa to more open-habitat taxa. The patterns observed here at a family level should be verified at the species level once species identifications are available. The extent to which such changes will increase or decrease overall diversity at the landscape scale will depend greatly on the spatial scale of removal of the woody vegetation.

Acknowledgments

This study was part of a national project on patterns and mechanisms of biodiversity in water-limited ecosystems, funded by the Israel Science Foundation (grant #1077/03), the Israel Ministry of Infrasctructure (Eshkol grant #3-2539), the Israel Nature and Parks Authority and Yad Hanadiv Foundation. N. Angel was supported by a fellowship from the Albert Katz School for Desert Studies, Ben-Gurion University of the Negev. N. Assaf was supported by a post-doctoral fellowship of the Blaustein Center for Scientific Cooperation and the Council for Higher Education. We thank especially I. Musli, E. Groner, A. Perevolotsky, G. Ne'eman and the many other participants in the project. This is publication no. 719 of the Mitrani Department of Desert Ecology.

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Arachnologische Mitteilungen 40: 94-104 Nuremberg, January 2011

Spatial and temporal structure of the spider community in the clay semi-desert of western Kazakhstan

Tatyana V. Piterkina

Abstract: The spatial and temporal structure of spider communities was studied in the clay semi-desert of the north-western Caspian Lowland, western Kazakhstan (49°23' N, 46°47' E). The soils and vegetation are complex, being composed of a mosaic of desert and steppe plant communities. Besides the native associations, there are plantations of different tree species. The ground-dwelling spider assemblages in the native habitats are the most diverse. The number of species inhabiting forest plantations is three times as small. Gnaphosidae is the leading family in the ground layer. They show high abundance and diversity levels during the whole season. Thomisidae, Lycosidae, Philodromidae, and Salticidae are abundant as well. The species diversity of herbage-dwelling spiders in different open native habitats is very similar. The spectrum of dominant families (Thomisidae, Oxyopidae, Araneidae, and Salticidae) and the seasonal dynamics of their ratio in desert and steppe associations have much in common. Spider assemblages of native and artificial habitats are characterised by change from multispecies polydominant spring-summer communities to impoverished imbalanced autumn ones. Seasonal changes in the species structure of mature spider groupings in native habitats are well pronounced, while the impact of seasonal conditions is even stronger than between-habitat differences. Complexes of typical species with different levels of habitat preference are revealed.

Key words: Araneae, ecology, habitat preference, seasonal dynamics

Spiders of steppe and semi-desert regions of the Palaearctic, unlike those of the temperate zone, are still poorly studied. There is some faunistic information (e.g. PONOMAREV 1981, 1988, 2005, 2008, PONOMAREV & TSVETKOVA 2003, PONOMAREV & TSVETKOV 2004a, 2004b, POLCHANINOVA 1992, 1995, 2002, KOVBLYUK 2006, EFIMIK et. al. 1997, ESYUNIN & EFIMIK 1998, ESYUNIN et al. 2007, TUNEVA & ESYUNIN 2003), but very little attention has been paid to such ecological aspects as the structure of populations, their dynamics, and the mechanisms of community function in arid and semi-arid conditions (ESYUNIN 2009).

This paper is focused on studying the spatial and temporal structure of spider assemblages in the clay semi-desert in the Volga and Ural rivers' interfluve. The research was carried out in the environs of the Dzhanybek Research Station of the Russian Academy of Sciences (49°23'N, 46°47'E), located on the border between the Western Kazakhstan Province of the Republic of Kazakhstan and the Volgograd Province of the Russian Federation. The area studied is a flat, nearly undrained plain in the north-western Caspian Lowland, a semi-desert zone (MILKOV & GVOZDETSKY 1986).

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submitted: 19.1.2010, accepted: 25.4.2010; online: 10.1.2011

Study area, material and methods

The Dzhanybek plain is the most arid area in the Ciscaspian semi-desert due to both internal drainage and soil salinity, despite its northernmost location. The climate of the territory is characterised by high atmospheric drought and aridity. Hot summers and severe winters are typical: the summer temperatures exceed 40°C, the winter temperatures sink lower than -35°C. The average annual air temperature (for 1951–2003) is 7.3°C; 18°C during the warm period and -3.5°C during the cold period. The average annual precipitation (for 1951-2003) is 295 mm, ranging from 44 (in 1984) to 354 mm (in 1993) (SAPANOV 2006). The sharp disparity of heat and moisture causes the very low humidity of the territory. The evaporative power reaches 1000 mm, which is 3 times the total rainfall. In addition, the meteorological conditions of the region are characterised by long-term fluctuations with regular cyclic reiterations of drought and moist periods (RODE 1959, LINDEMAN et al. 2005, SAPANOV 2006).

Another characteristic feature of the study area is a well pronounced complex pattern of soils and vegetation, with a combination of typical desert, semi-desert and steppe habitats. The co-existence of such

contrasting biotopes is caused by pronounced microrelief and, consequently, differences in moisture, soil substrates and their properties (RODE & POLSKIKH 1961).

Microelevations are occupied by plant communities of the desert type, with *Kochia prostrata*, *Artemisia pauciflora*, and *Salsola laricina* on saline soils. The groundwater is saline. Forb-grass vegetation (*Stipa* spp., *Festuca valesiaca*, *Agropyron cristatum*, etc.) on dark chestnut and meadow chestnut soils with fresh groundwater occupies microdepressions (down to 0.4 m deep); they represent steppe habitats. This mosaic of elements constitutes most of the territory. Large depressions (down to 1-1.5 m deep, area of 1-100 hectares) with steppe plant communities take up about 10–15 % of the area. These large depressions are best supplied with water, due to runoff from the surrounding area. Besides these mentioned native associations, there are 50-year-old plantations composed of different tree species.

Material for this work was collected by the author (April-October 2004-2005) and Dr. K.G. Mikhailov (June-September 1984) in three native habitats (desert associations of microelevations, and steppe associations of large depressions, and microdepressions) and three artificial ones: oak (*Quercus robur*) forest belts, oak patch in a park, and elm (*Ulmus pumila*) forest belts. The collections in the latter habitat took place only in 1984. In recent years, the vitality of the forest-belt has become very poor; the trees are very sparse so the conditions in it have approached those of an open habitat.

Traditional collecting methods were used: pitfall trapping (one transect – 10 traps), hand-sorting of soil and litter samples (0.25 x 0.25 m, 10 samples) and sweeping (one sample – 4 x 25 sweeps, 3 times a day, at 00:00, 8:00 and 16:00). Sampling was carried out every 7-10 days. Pitfall traps were set in microelevations, microdepressions and woody plantations. Soil and litter samples were taken in all studied habitats. As the plantations had a rather poor and scattered herbaceous layer, sweeping was undertaken only in native habitats.

The material includes a total of 15000 pitfall days, 570 soil and litter samples, and 268 sweeping samples.

One of the most important features of the spider population in the clay semi-desert is its strongly pronounced seasonality and vertical stratification. Thus, I analysed the structure of spider complexes separately by layer, i.e. ground and herbaceous layers, and seasons, i.e. spring, summer and autumn. When calculating the ratio of families, I considered spiders of all instars. With respect to the seasonal changes in species compositions I used mature spiders only, although I suggest that the differences revealed might reflect certain phenological trends.

Taxa with a relative abundance of ≥5 % were considered predominat. The habitat preference of species was calculated using Pesenko's coefficient (F_{ij}) (PESENKO 1982), which represents a mathematical transformation of the share of a species in a single biotope to its share in all other biotopes:

$$F_{ij} = (n_{ij}/N_j - n_i/N)/(n_{ij}/N_j + n_i/N),$$

where n_{ij} – number of specimens of *i*-species in samples from *j*-biotope with total volume N_j; n_i – number of specimens of *i*-species in all other biotopes with total volume *N*. Single records of species were omitted from the calculation.

The choice of this coefficient was based on the variety of the collecting methods used, which caused the heterogeneity of the data obtained and the difficulties in their unification. Using relative indices (not absolute ones) simplifies the interpretation of data and makes miscellaneous information comparable. The value of the coefficient ranges from –1 (absolute avoidance) to +1 (absolute preference).

Statistical data analysis was performed using Statistica 6.0.

Results

About 20000 spider specimens were captured and studied, with about 7000 of these spiders being mature. Altogether, 172 species from 88 genera and 21 families were recovered. Taking into account the scant information published previously, the spider fauna of the Dzhanybek Station amounts to 184 species from 93 genera and 22 families. A checklist and the distribution of species between the study habitats has been made available elsewhere (PITERKINA 2009, PITERKINA & MIKHAILOV 2009). Since the time of these mentioned papers some taxonomical changes have taken place or some identifications were refined, thus some species names may not coincide. Namely, *Ero* sp. turned out to be *Ermetus inopinabilis* Ponomarev, 2008, *Theridion* cf. *uhligi* Martin, 1974 – *T. uhligi*, *Thanatus constellatus* Charitonov, 1946 – *T. oblongiusculus* (Lucas, 1846), and *Eresus cinnaberinus* (Olivier, 1789) – *E. kollari* Rossi, 1846.

Species structure of spider communities and its seasonal dynamics

The communities of ground-dwelling spiders in the native habitats – microelevations and microdepressions – are the most diverse (about 90 species). The number of species inhabiting forest plantations is three times as small (about 30 species) (Tab. 1).

The activity of spiders in the open habitats fluctuates from 20 to 70 ind. / 100 pitfall-days, with the highest numbers in spring and summer. The amplitude of its fluctuation is much higher in the forest plantations (from 3-4 to 100 ind./100 pitfall-days). The density of the spider population, based on soil and litter samples, reaches its highest values in autumn (up to 117 ind. /m^2).

Gnaphosidae is the dominant family in the native associations. They exhibit high abundance and diversity levels (about 50 %) during the whole vegetation season, this being quite typical of arid and semi-arid landscapes. The proportions of Lycosidae and Salticidae are less, but also stable. Linyphiidae predominate in spring and autumn, Oxyopidae in summer, Titanoecidae in spring and summer, Thomisidae in summer and autumn. The dominant complex of the tree plantations is less diverse. The proportion of Gnaphosidae is significantly lower than in native habitats (about 20–30 %), while the abundance of Thomisidae is high and stable during the entire vegetation season (about 30–50 %). Pisauridae show a peak in their abundance in spring and autumn, whereas Liocranidae peak in summer.

Seasonal change in species dominance is well pronounced and the species set is relatively stable across different years (Tab. 1). For example, in the desert habitats, *T. veteranica*, *Haplodrassus* cf. *soerenseni*, *E. eltonica*, *D. rostratus*, *Z. orenburgensis* predominate in spring populations in both years of study. The stable summer dominants are *P. braccatus*, *H. horridus*, *Oxyopes* cf. *xinjiangensis*, *D. rostratus* and *Z. orenburgensis*. The autumn populations are rather imbalanced. Characteristic is a high level of predominance of 1-2 species that can change in different years (*Z. orenburgensis*, *X. marmoratus* or *D. rostratus*). The dominant complexes of oak plantations have much in common and include several species abundant during the whole vegetation season (*Z. gallicus*, *O. praticola*, *X. luctator*) (Tab. 1). The species diversity of herbage-dwelling spiders in the open native habitats is very similar: about 50 species (Tab. 2). The abundance of hortobiotic spiders fluctuates with a high amplitude, reaching its maximum in summer (about 100 ind. / 100 sweeps). The spectrum of predominating families and the seasonal dynamics of their proportion in desert and steppe associations have much in common. Uloboridae and Linyphiidae are abundant in spring, Araneidae and Oxyopidae in spring and autumn, Salticidae in sum-

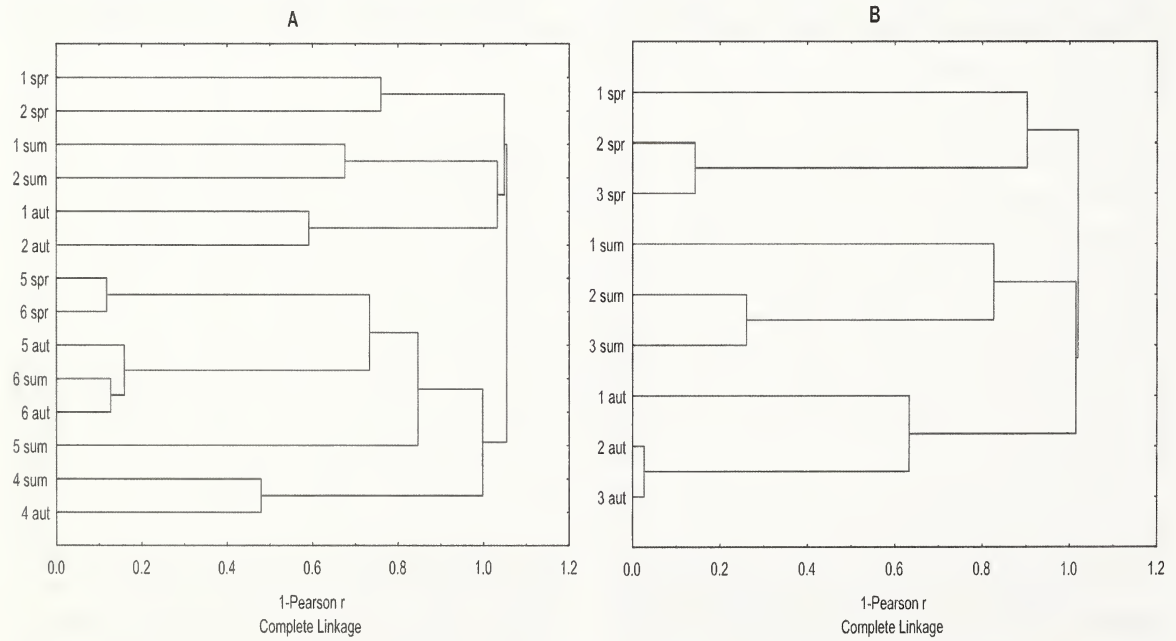

Figure 1: Clustering the mature spider complexes for separate seasons: A – ground-dwelling spiders, B – herbage-dwelling spiders. Habitats: 1: microelevations, 2: microdepressions, 3: large depressions, 4: elm shelter-belt, 5: oak shelter-belt, 6: oak patch in a park. Seasons: spr – spring, sum – summer, aut – autumn.

mer and autumn. Philodromidae, Clubionidae and Miturgidae are numerous during the whole vegetative period.

The seasonal change of the predominant complexes of species is also well-pronounced (Tab. 2). In spring and, especially, summer, the sets of abundant species are not stable in different years. On the contrary, the autumn populations of all habitats are very similar. They are mainly formed by two species, *Xysticus marmoratus* and *X. striatipes*. Co-dominance of *Cheiracanthium* cf. *virescens* adds originality to the autumn assemblages of microelevations, *E. michailovi* to those of microdepressions, and *H. lineiventris* to those of large depressions (Tab. 2).

Clustering the mature spider complexes for separate seasons (Fig. 1) yielded interesting results. Two large clusters were revealed among ground-dwelling spiders: assemblages of native biotopes and of forest plantations (Fig. 1A). Within them, the populations were not united by habitat, as one would expect, but by season. The cluster of open habitats includes populations of microelevations and microdepressions during spring, summer and autumn. Microclimatic conditions in woody plantations were presumably comparatively smoother, even though no direct abiotic measurements were taken. The cluster of artificial forests appears to be less differentiated. The same tendency is also obvious when clustering the herbage-dwelling spider complexes: three pronounced clusters united spring, summer and autumn assemblages of microelevations, microdepressions and large depressions respectively (Fig. 1B).

Habitat preferences of species

Spider assemblages of desert associations are the most specific. The share of species collected only in microelevations is highest (24 %), whereas it is half this in the other biotopes. Most of unique species, with few exceptions, exhibit low abundance levels and hardly play coenotic roles (Tab. 3).

Table 1: Species structure of populations of mature ground-dwelling spiders. Numbers in brackets show relative abundance in %.

Microelevations (desert habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	45	39	49	99 32	24	22	13
Predominating species	*Titanoeca veteranica* (12) *Haplodrassus* cf. *soerenseni* (8) *Micaria pallipes* (7) *Evippa eltonica* (6) *Drassodes rostratus* (6) *Gnaphosa steppica* (5) *Zelotes orenburgensis* (5)	*Evippa eltonica* (34) *Titanoeca veteranica* (13) *Haplodrassus* cf. *soerenseni* (10) *Zelotes orenburgensis* (5)	*Heriaeus horridus* (14) *Oxyopes* cf. *xinjiangensis* (14) *Zelotes orenburgensis* (13) *Gnaphosa steppica* (9) *Evippa eltonica* (9) *Phaeocedus braccatus* (8) *Drassodes rostratus* (6)	*Gnaphosa lucifuga* (16) *Phaeocedus braccatus* (11) *Heriaeus horridus* (10) *Nurscia albomaculata* (10) *Zelotes orenburgensis* (9) *Drassodes rostratus* (9) *Oxyopes* cf. *xinjiangensis* (6)	*Zelotes orenburgensis* (48) *Drassodes rostratus* (21) *Ozyptila lugubris* (7)	*Xysticus marmoratus* (44) *Thanatus pictus* (18) *Xysticus striatipes* (7) *Drassodes rostratus* (7) *Zelotes orenburgensis* (5)	*Drassodes rostratus* (36) *Xysticus marmoratus* (21) *Zelotes orenburgensis* (17) *Talanites strandi* (5)

Microdepressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	46	40	17	84 38	6	29	24
Predominating species	*Thanatus arenarius* (15) *Berlandina cinerea* (11) *Zelotes electus* (11) *Haplodrassus kulczynskii* (8) *Gnaphosa taurica* (6) *Alopecosa taeniopus* (5)	*Berlandina cinerea* (20) *Thanatus arenarius* (19) *Gnaphosa taurica* (11) *Haplodrassus* cf. *soerenseni* (7) *Haplodrassus kulczynskii* (6) *Zelotes electus* (6) *Haplodrassus signifer* (5)	*Xysticus ninnii* (26) *Thanatus atratus* (14) *Aelurillus v-insignitus* (14) *Zelotes electus* (6)	*Xysticus ninnii* (12) *Berlandina cinerea* (11) *Gnaphosa lucifuga* (10) *Thanatus atratus* (10) *Zelotes caucasius* (7) *Gnaphosa steppica* (6) *Gnaphosa taurica* (5) *Nurscia albomaculata* (5)	*Phlegra bicognata* (36) *Aelurillus v-insignitus* (27)	*Thanatus pictus* (20) *Xysticus marmoratus* (19) *Xysticus striatipes* (15) *Haplodrassus isaevi* (14) *Trichopterna cito* (7)	*Alopecosa schmidti* (13) *Xysticus striatipes* (13) *Xysticus marmoratus* (12) *Thanatus pictus* (7)

Elm shelter-belt

Characteristics	1984	
	Summer	Autumn
Number of species	30	
	26	11
Predominating species	*Xysticus ninnii* (22) *Zelotes gallicus* (16) *Titanoeca schineri* (9) *Pardosa xinjiangensis* (8) *Drassyllus pusillus* (8) *Pisaura mirabilis* (5)	*Zelotes gallicus* (44) *Gnaphosa taurica* (28)

Oak shelter-belt

Characteristics	Spring		Summer	Autumn	
	2004	2005	2004	2004	2005
Number of species	39				
	14	18	17	9	5
Predominating species	*Pisaura mirabilis* (31) *Drassyllus pusillus* (14) *Zelotes gallicus* (13) *Ozyptila praticola* (11) *Gnaphosa taurica* (6) *Xysticus luctator* (6) *Zora pardalis* (6)	*Xysticus luctator* (39) *Pisaura mirabilis* (18) *Ozyptila praticola* (10) *Zora pardalis* (9) *Drassyllus pusillus* (8) *Zelotes gallicus* (8)	*Titanoeca schineri* (42) *Pisaura mirabilis* (9) *Zora pardalis* (8) *Zelotes gallicus* (7) *Ozyptila praticola* (7) *Xysticus ninnii* (7) *Oxyopes lineatus* (5) *Xysticus luctator* (5)	*Ozyptila praticola* (43) *Alopecosa taeniopus* (24)	*Ozyptila praticola* (44) *Zelotes longipes* (22) *Xysticus luctator* (22) *Zelotes gallicus* (11)

Oak patch in a park

Characteristics	Spring		Summer	Autumn	
	2004	2005	2004	2004	2005
Number of species	31				
	17	17	13	5	4
Predominating species	*Xysticus luctator* (19) *Ozyptila praticola* (18) *Zelotes gallicus* (15) *Pisaura mirabilis* (12) *Drassyllus pusillus* (12) *Gnaphosa taurica* (6)	*Xysticus luctator* (45) *Drassyllus pusillus* (15) *Ozyptila praticola* (12) *Pisaura mirabilis* (5)	*Ozyptila praticola* (45) *Titanoeca schineri* (13) *Drassyllus pusillus* (12) *Sitticus zimmermanni* (6) *Xysticus luctator* (5) *Xysticus robustus* (5)	*Ozyptila praticola* (78) *Sitticus zimmermanni* (11) *Berlandina cinerea* (6) *Zelotes electus* (6)	*Zelotes gallicus* (27) *Aelurillus v-insignitus* (27) *Agroeca cuprea* (27) *Ozyptila praticola* (18)

Table 2: Species structure of populations of mature herbage-dwelling spiders. Numbers in brackets shows relative abundance in %.

Microelevations (desert habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	48						
	24	14	14	20	3	8	4
Predominating species	*Lasaeola tristis* (15) *Gibbaranea bituberculata* (14) *Microlinyphia pusilla* (9) *Agyneta saaristoi* (8) *Archaeodictyna consecuta* (7) *Cheiracanthium* cf. *virescens* (6) *Uloborus walckenaerius* (5)	*Gibbaranea bituberculata* (21) *Clubiona genevensis* (13) *Lasaeola tristis* (13) *Alopecosa cronebergi* (8) *Robertus arundineti* (8)	*Oxyopes* cf. *xinjiangensis* (61) *Dictyna latens* (8) *Cheiracanthium* cf. *virescens* (6) *Aculepeira armida* (6)	*Oxyopes* cf. *xinjiangensis* (24) *Micaria pallipes* (12) *Thanatus constellatus* (12) *Dictyna latens* (10) *Pellenes albopilosus* (6) *Gibbaranea bituberculata* (6) *Lasaeola tristis* (6)	*Xysticus striatipes* (69) *Oxyopes* cf. *xinjiangensis* (23) *Dictyna latens* (7)	*Xysticus marmoratus* (60) *Cheiracanthium* cf. *virescens* (19) *Xysticus striatipes* (9)	*Xysticus marmoratus* (65) *Xysticus striatipes* (25) *Thanatus constellatus* (5) *Cheiracanthium* cf. *virescens* (5)

Microdepressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	53						
	29	14	23	21	5	11	6
Predominating species	*Gibbaranea bituberculata* (21) *Evarcha michailovi* (16) *Trichopterna cito* (11) *Clubiona genevensis* (10) *Cheiracanthium* cf. *virescens* (6)	*Cheiracanthium* cf. *virescens* (32) *Clubiona genevensis* (15) *Thanatus arenarius* (10) *Trichopterna cito* (8) *Gibbaranea bituberculata* (5) *Mangora acalypha* (5) *Philodromus histrio* (5) *Microlinyphia pusilla* (5)	*Heliophanus lineiventris* (13) *Thanatus mikhailovi* (13) *Heliophanus koktas* (9) *Aculepeira armida* (8) *Cheiracanthium* cf. *virescens* (7) *Cheiracanthium pennyi* (6) *Xysticus ninnii* (5) *Dictyna latens* (5) *Uloborius walckenaerius* (5)	*Thanatus constellatus* (23) *Neoscona adianta* (8) *Xysticus marmoratus* (8) *Thanatus atratus* (8) *Evarcha michailovi* (6) *Thomisus onustus* (6) *Oxyopes lineatus* (6)	*Xysticus striatipes* (73) *Cercidia levii* (18) *Heliophanus koktas* (5)	*Xysticus striatipes* (57) *Evarcha michailovi* (16) *Xysticus marmoratus* (12) *Cercidia levii* (5)	*Xysticus striatipes* (78) *Evarcha michailovi* (9) *Xysticus marmoratus* (7)

Big depressions (steppe habitats)

Characteristics	Spring		Summer		Autumn		
	2004	2005	1984	2004	1984	2004	2005
Number of species	52						
	19	11	18	20	12	8	6
Predominating species	*Gibbaranea bituberculata* (33) *Uloborius walckenaerius* (11) *Cheiracanthium* cf. *virescens* (9) *Agyneta* spp. (♀) (6) *Trichopterna cito* (6) *Archaeodictyna consecuta* (6)	*Cheiracanthium* cf. *virescens* (35) *Evarcha michailovi* (19) *Cheiracanthium pennyi* (12) *Philodromus histrio* (8)	*Aculepeira armida* (27) *Dictyna latens* (16) *Oxyopes* cf. *xinjiangensis* (10) *Heliophanus lineiventris* (8) *Thanatus oblongiusculus* (8) *Cheiracanthium* cf. *virescens* (5)	*Thanatus oblongiusculus* (34) *Oxyopes lineatus* (16) *Neoscona adianta* (9) *Oxyopes heterophthalmus* (9) *Thomisus onustus* (6)	*Xysticus striatipes* (56) *Xysticus marmoratus* (15)	*Xysticus striatipes* (62) *Xysticus marmoratus* (18) *Heliophanus lineiventris* (7)	*Xysticus striatipes* (70) *Heliophanus lineiventris* (19)

Table 3: Unique species per type of habitat.

	number	%
Microelevations	28	23.7
Microdepressions	10	8.9
Large depressions	7	13.4
Elm shelter-belt	3	10.3
Oak shelter-belts	6	15.4
Oak patch in a park	4	12.9

As many as 25 species occur in all native habitats, another five in all forest plantations. Two species, *Lathys stigmatisata* and *Xysticus ninnii*, are ubiquitous and inhabit all studied habitats.

However, finding the species in a particular habitat does not necessarily indicate habitat preference. In order to estimate preference level, Pesenko's coefficient (F_{ij}) was used. A complex of species, including taxa both with high ($F_{ij} \geq 0.7$) and relatively low ($0.3 \geq F_{ij} > 0.7$) levels of habitat preference, was revealed for each habitat (Tab. 4).

Discussion

It is well known that the denser the vegetation the greater is density of spiders, and the greater the diversity of vegetation the greater the spider species diversity (DUFFEY 1962). But the spider assemblages of both the ground and herbaceous layers of open native habitats (microelevations, microdepressions and large depressions) are very similar not only in species diversity but also in density. This was rather surprising as the low, sparse and rather poor desert plant communities look much more miserable compared to the dense forb-grass vegetation of steppe habitats. This reveals a complex of species well adapted to the extreme conditions of desert associations. On the contrary, the communities of forest plantations appear to be significantly impoverished. The poorness of soil fauna under Dzhanybek plantations was demonstrated for other arthropods as well (CHERNOVA 1971, KRIVOLUTSKII 1971, etc.).

Calculating the level of habitat preference (F_{ij}) revealed complexes of typical species for each habitat (Tab. 4). In spite of mosaic structure and a comparatively small size of desert and steppe elements (some tens of square meters) in complex Northern Caspian semi-desert, the spider groupings formed on them are rather specific and contain sets of species associated with the particularities of the substrate (soil) and vegetation of those elements. The complexes of typical species of native habitats – microelevations and microdepressions – are the richest (35-40 species). Most of the typical species in desert associations are dwellers of arid and semi-arid landscapes: these are steppe (*D. rostratus*, *Z. orenburgensis*, *G. steppica*, etc.), semi-desert (*S. crassipedis*, *T. mikhailovi*, *W. stepposa*) and steppe-desert species (*H. horridus*, *O. lugubris*); with some participation of nemoral-steppe and nemoral ones. The share of steppe species (*B. cinerea*, *G. leporina*, *H. isaevi*, etc.) decreases significantly in associations of microdepressions and large depressions, while nemoral-steppe (*E. michailovi*, *Z. electus*, *T. arenarius*, etc.) and nemoral-subtropical species (*P. chrysops*, *P. fasciata*, *A. lobata*, etc.) prevail. Most of the typical species are quite abundant and predominate in these biotopes.

In addition, there is a complex of species which can inhabit several types of native habitats with similar probability levels (except for woody plantations). These are *Trichoncoides* cf. *piscator*, *G. bituberculata*, *A. v-insignitus*, *A. cursor*, *P. histrio*, *Z. segrex*, etc.

Complexes of typical species of woody plantations are poor and include 12-15 species, although the level of habitat preference is very high (Tab. 4). Most of them are nemoral species. Populations in the plantations are very likely composed of highly eurytopic species (*D. pusillus*, *Z. gallicus*, *P. mirabilis*) and typical dwellers of intrazonal associations (*S. zimmermanni*, *T. schineri*) with a small participation of forest species (*O. praticola*) which could be introduced with plant material.

On the other hand, the structure of spider assemblages is heavily determined by macroclimatic conditions and their seasonal changes. The analysis of seasonal features of population structure shows that the spring and summer spider assemblages of both ground and herbaceous layers are characterised by high species diversity levels and a relatively high number of predominating species, as opposed to the impoverished, imbalanced autumn populations (Tab. 1-2). The same pattern was recovered by ESYUNIN (2009) for spiders of steppe and steppe-like habitats in the Ural Mountains.

Clustering the spider complexes for separate seasons confirmed the prevailing role of seasonal differences in species proportions for mature spider groupings of native habitats when comparing between-habitat differences (Fig. 1). The populations of native associations were not united by habitats, but by seasononality. A similar trend has been also shown by ESYUNIN (2009) for the spider populations of steppe-like habitats in the Ural Mountains.

It is interesting to note that such a tendency was

Table 4: Pesenko's coefficient of a habitat preference (*Fij*) of spiders. Species are grouped according to their preference to a certain habitat. Within the groups species are ranked in order of decreasing the values of *Fij*. Grey background: high level of habitat preference ($0.7 \leq F_{ij} \leq 1.00$); bold: relatively low level of habitat preference ($0.3 \leq F_{ij} < 0.7$). Habitats as in Fig. 1.

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Chalcoscirtus nigritus	17	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Heriaeus horridus	54	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Lepthyphantes spasskyi	7	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Micaria guttulata	7	**1.00**	-1.00		-1.00	-1.00	-1.00
Nomisia aussereri	4	**1.00**	-1.00		-1.00	-1.00	-1.00
Robertus arundineti	5	**1.00**	-1.00	-1.00	-1.00	-1.00	-1.00
Urozelotes sp.	4	**1.00**	-1.00		-1.00	-1.00	-1.00
Evippa eltonica	189	**0.98**	-0.94		-1.00	-1.00	-1.00
Titanoeca veteranica	115	**0.96**	-0.90		-1.00	-1.00	-1.00
Zelotes orenburgensis	204	**0.93**	-0.82		-1.00	-0.94	-1.00
Drassodes rostratus	153	**0.91**	-0.78	-1.00	-1.00	-0.92	-1.00
Lasaeola tristis	23	**0.91**	-0.75	-0.85			
Phaeocedus braccatus	47	**0.91**	-0.77		-1.00	-1.00	-1.00
Micaria pallipes	56	**0.89**	-0.71	-1.00	-1.00	-1.00	-1.00
Oxyopes cf. *xinjiangensis*	114	**0.82**	-0.92	-0.36	-1.00	-1.00	-1.00
Thanatus mikhailovi	22	**0.80**	-0.51	-1.00	-1.00	-1.00	-1.00
Microlinyphia pusilla	16	**0.71**	-0.26	-0.76	-1.00	-1.00	-1.00
Silometopus crassipedis	23	**0.71**	-0.35	-0.59	-1.00	-1.00	-1.00
Talanites mikhailovi	10	**0.71**	-0.35		-1.00	-1.00	-1.00
Trachyzelotes adriaticus	5	**0.71**	-0.35		-1.00	-1.00	-1.00
Talanites strandi	14	**0.69**	-0.31		-1.00	-1.00	-1.00
Xysticus marmoratus	278	**0.66**	-0.44	-0.41	-1.00	-1.00	-1.00
Gnaphosa lucifuga	79	**0.65**	-0.23	-1.00	-1.00	-1.00	-1.00
Theridion uhligi	6	**0.64**	-0.21		-1.00	-1.00	-1.00
Ozyptila lugubris	19	**0.62**	-0.18		-1.00	-1.00	-1.00
Theridion innocuum	8	**0.62**	-0.26	-0.54	-1.00	-1.00	-1.00
Drassyllus sur	33	**0.60**	-0.16		-1.00	-1.00	-1.00
Nurscia albomaculata	36	**0.59**	-0.15		-1.00	-1.00	-1.00
Ozyptila pullata	22	**0.58**	-0.13	-1.00	-1.00	-1.00	-1.00
Pellenes albopilosus	26	**0.57**	-0.11	-0.63	-1.00	-1.00	-1.00
Archaeodictyna consecuta	18	**0.53**	-0.41	-0.18			
Ceratinella brevis	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Euophrys frontalis	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Gnaphosa steppica	72	**0.50**	-0.08		-1.00	-0.83	-0.77
Walckenaeria stepposa	3	**0.50**	-0.02		-1.00	-1.00	-1.00
Haplodrassus cf. *soerenseni*	102	**0.42**	0.05		-1.00	-0.88	-0.83
Aelurillus m-nigrum	5	**0.39**	0.13		-1.00	-1.00	-1.00
Cheiracanthium cf. *virescens*	99	**0.36**	-0.15	-0.20	-1.00	-1.00	-1.00
Phlegra bicognata	24	**0.36**	0.16		-1.00	-1.00	-1.00
Uloborus walckenaerius	26	**0.35**	-0.22	-0.12	-1.00	-1.00	-1.00
Zelotes caucasius	39	**0.32**	0.10		-0.08	-0.71	-1.00
Improphantes contus	7	-1.00	**1.00**		-1.00	-1.00	-1.00
Heliophanus flavipes	4	-1.00	**1.00**	-1.00			
Phlegra fasciata	10	-1.00	**1.00**	-0.05	-1.00	-1.00	-1.00
Walckenaeria alticeps	4	-1.00	**1.00**	-1.00	-1.00	-1.00	-1.00
Haplodrassus kulczynskii	48	-0.94	**0.98**		-1.00	-1.00	-1.00
Trichopterna cito	169	-0.98	**0.96**	-0.43	-0.19	-0.91	-1.00
Berlandina cinerea	139	-0.83	**0.92**		-1.00	-1.00	-0.76
Cercidia levii	37	-1.00	**0.92**	-0.80	-1.00	-1.00	-1.00
Trichoncus villius	28	-0.79	**0.92**	-1.00	-1.00	-1.00	-1.00
Thanatus arenarius	140	-0.76	**0.90**	-0.54	-1.00	-0.91	-1.00
Zelotes electus	73	-0.96	**0.90**		**0.31**	-0.83	-0.77
Haplodrassus isaevi	37	-0.69	**0.88**		-1.00	-1.00	-1.00

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Gnaphosa leporina	24	-1.00	**0.81**		-1.00	-1.00	0.30
Thanatus atratus	45	-0.52	**0.81**	**0.40**	-1.00	-1.00	-1.00
Zelotes longipes	60	-0.62	**0.79**		-0.29	-0.63	-1.00
Evarcha michailovi	77	-0.92	**0.77**	-0.52	-1.00	-1.00	-1.00
Heliophanus koktas	19	-1.00	**0.77**	-0.50			
Pardosa plumipes	5	-0.45	**0.77**		-1.00	-1.00	-1.00
Drassodes lapidosus	4	-0.33	**0.71**		-1.00	-1.00	-1.00
Clubiona genevensis	27	-0.26	**0.66**	-0.74	-1.00	-1.00	-1.00
Drassodes villosus	7	-0.25	**0.66**		-1.00	-1.00	-1.00
Alopecosa schmidti	31	-0.24	**0.65**		-1.00	-1.00	-1.00
Thanatus pictus	96	-0.11	**0.57**	-0.16	-1.00	-1.00	-1.00
Thanatus sp.	8	0.00	**0.49**	-0.05	-1.00	-1.00	-1.00
Alopecosa taeniopus	41	-0.65	**0.47**		0.25	0.30	-0.63
Agyneta saaristoi	30	-0.05	**0.43**	-0.54	-1.00	-0.39	-1.00
Haplodrassus signifer	45	0.05	**0.42**		-1.00	-1.00	-0.65
Eresus kollari	13	0.13	**0.39**		-1.00	-1.00	-1.00
Gnaphosa taurica	135	-0.31	**0.38**		**0.35**	-0.36	-0.10
Xysticus striatipes	426	-0.60	**0.35**	-0.03	-0.29	-0.80	-1.00
Agroeca maculata	61	0.15	**0.33**		-1.00	-1.00	-0.73
Philaeus chrysops	5	0.20	**0.32**	-1.00	-1.00	-1.00	-1.00
Simitidion simile	9	0.12	**0.32**	-0.54	-1.00	-1.00	-1.00
Scotargus pilosus	4	0.20	**0.32**		-1.00	-1.00	-1.00
Xysticus cristatus	43	0.20	**0.32**	0.22	-1.00	-1.00	-1.00
Trichoncoides cf. *piscator*	11	**0.41**	**0.32**	-1.00	-1.00	-1.00	-1.00
Zelotes segrex	15	0.26	0.26		-1.00	-1.00	-1.00
Aelurillus v-insignitus	30	0.20	0.13		-1.00	-1.00	0.01
Alopecosa cursor	34	0.26	0.27		-1.00	-1.00	-1.00
Gibbaranea bituberculata	82	0.09	0.02	-0.10	-1.00	-1.00	-0.90
Philodromus histrio	18	-0.01	-0.11	0.12	-1.00	-1.00	-0.90
Oxyopes lineatus	43	-1.00	-0.62	**0.84**	-1.00	-1.00	-1.00
Neoscona adianta	23	-1.00	-0.42	**0.73**			
Argiope lobata	4	0.03	-1.00	**0.69**			
Thanatus oblongiusculus	99	-0.51	-0.53	**0.67**			
Aculepeira armida	53	-0.49	-0.53	**0.66**	-1.00	-1.00	-1.00
Oxyopes heterophthalmus	29	-0.60	-0.43	**0.64**	-1.00	-1.00	-1.00
Thomisus onustus	20	-0.71	-0.23	**0.54**			
Dictyna latens	45	0.02	-0.63	**0.50**			
Agyneta spp. (♀)	29	-0.01	-0.38	**0.34**	-1.00	-0.25	-0.09
Heliophanus lineiventris	75	-0.38	0.01	0.22	-1.00	-1.00	-1.00
Heriaeus melloteei	10	-0.04	-0.15	0.18	-1.00	-1.00	-1.00
Pardosa xinjiangensis	6	-1.00	-1.00		**1.00**	-1.00	-1.00
Micaria rossica	7	-0.25	-0.13		**0.92**	-1.00	-1.00
Pseudeuophrys obsoleta	5	-1.00	-1.00		**0.91**	**0.63**	**0.40**
Ermetus inopinabilis	8	-0.33	-1.00		**0.90**	**0.59**	-1.00
Titanoeca quadriguttata	3	-1.00	-0.02		**0.88**	**0.53**	-1.00
Zelotes atrocaeruleus	6	-0.14	-0.02		**0.88**	-1.00	-1.00
Xysticus ninnii	85	-0.79	0.24	0.22	**0.86**	0.04	-0.42
Tibiaster djanybekensis	24	**0.56**	-1.00	-1.00	**0.83**	-0.49	-1.00
Zelotes gallicus	96	-1.00	-1.00		**0.83**	**0.75**	**0.47**
Mangora acalypha	5	0.23	**0.49**	-1.00	**0.69**	-1.00	-1.00
Cheiracanthium pennyi	24	-1.00	0.10	0.10	-1.00	**1.00**	-1.00
Pisaura mirabilis	105	-1.00	-1.00		0.13	**0.91**	**0.37**
Zora pardalis	56	-1.00	-0.68		0.10	**0.88**	0.28
Lathys stigmatisata	93	-0.80	-0.25	-0.25	0.21	**0.70**	**0.37**
Titanoeca schineri	73	-1.00	-1.00		**0.55**	**0.87**	**0.44**
Xysticus luctator	198	-1.00	-0.98		-1.00	**0.73**	**0.80**

Species	Number of specimens	Habitats					
		1	2	3	4	5	6
Drassyllus pusillus	90	-1.00	-1.00		**0.40**	**0.63**	**0.83**
Sitticus zimmermanni	29	-1.00	-0.87		**0.42**	**0.55**	**0.84**
Ozyptila praticola	155	-1.00	-1.00	-1.00	-1.00	**0.60**	**0.88**
Xysticus robustus	10	-1.00	-1.00	-1.00	-1.00	**0.68**	**0.84**
Zelotes subterraneus	3	-1.00	-1.00		-1.00	-1.00	**1.00**
Philodromus cespitum	5	-1.00	0.10	0.10	-1.00	-1.00	**1.00**
Agroeca cuprea	4	-1.00	-1.00		-1.00	-1.00	**1.00**

not revealed for snout-beetles (Coleoptera, Curculionoidae) investigated at the Dzhanybek Station during the same period. These phytophagous insects showed that the influence of between-habitat differentiation on the structure of their populations – which was determined by their close links with the plants on which they forage (KHRULEVA et al. in press) – was much stronger than seasonal changes. Spiders being a group of mobile generalist predators are more likely to be influenced by abiotic factors.

Acknowledgements

I would like to thank the managers of the Dzhanybek Research Station for the opportunity to work there. I am also thankful to Kirill G. Mikhailov for the material he collected in 1984 and for his valuable advice, as well as to the following arachnologist colleagues, Galina N. Azarkina, Alexander V. Gromov, Dmitri V. Logunov, Yuri M. Marusik, Vladimir I. Ovtsharenko, and Andrei V. Tanasevitch for their help in identifying some of the spider taxa. I am deeply indebted to all staff of the Laboratory of Synecology for their constant help and encouragement. Sergei I. Golovatch kindly checked the English of an advanced draft.

The study was supported by the Russian Foundation for Basic Research, the Program "The Origin and Evolution of the Biosphere", the Program for the Support of the Leading Academic Schools and Young Scientists.

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Arachnologische Mitteilungen 40: 105-109 Nuremberg, January 2011

Regional variations in agrobiont composition and agrobiont life history of spiders (Araneae) within Hungary

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doi: 10.5431/aramit4012

Abstract: Agrobiont spider species are well adapted to arable systems, which have fairly uniform vegetation structure and pest assemblages over continent-wide areas. We wanted to study, whether agrobiont spider sub-assemblages and the life history of the most prominent agrobiont, *Pardosa agrestis,* show any regional variation within Hungary, where only modest climatic differences exist between the NW and SE parts of the country. We studied agrobiont species of spider assemblages in 27 alfalfa and 21 cereal fields with suction sampling and pitfalls. The similarity structure of these agrobiont sub-assemblages (Sørensen distance measure) was congruent with the geographic distance matrices (Eucledian distance), as tested by Mantel tests. However, if we considered sub-assemblages consisting of the non-agrobiont species, this congruency was always higher. Thus, agrobionts responded only moderately to geographical variation if we compare them to non-agrobiont species. We studied the generation numbers and the occurrence of the first adult individuals in *P. agrestis;* the most common agrobiont spider in Hungary. This comparison involved comparing fields along a NW – SE gradient during 6 sampling years in pairwise comparisons, where in each year a northern and a southern population was compared with a minimum distance of 126 km in between. In generation numbers there was no difference; we found two generations across Hungary. In contrast, the first occurrence of adult individuals was on average 15 days earlier in both generations in the more southern populations. Thus, it can be concluded that agrobionts show a fairly stable and relatively low magnitude response over country-sized geographical ranges.

Key words: alfalfa, biological control, cereal, climatic gradient, natural enemy, *Pardosa agrestis*, regionality

Agrobiont spider species are well adapted to arable systems (SAMU & SZINETÁR 2002, KAJAK & OLESZCZUK 2004). Agricultural crops have a fairly uniform vegetation structure and pest assemblages over continent-wide areas (WECHSUNG et al. 1995). It is interesting to see how this large scale homogenisation of habitat structure affects spiders. On the one hand, the same crop might attract different spiders from the local fauna, whose species might contribute differently to the biological control potential of the natural enemy complex (BATÁRY et al. 2008, SAMU et al. 2008). On the other hand, uniform and low diversity spider assemblages of large crop areas might negatively affect nearby local natural assemblages (JEANNERET et al. 2003). Thus, information about the regional variation of crop spider assemblages is important both from biological control and nature conservation perspectives. Previous data indicates that spider assemblages even on the same crop plants vary within Europe (HÄNGGI et al. 1995, FINCH et al. 2008). However, the extent and scale of this variation is largely unknown.

Pardosa agrestis is the most common (c. 40 % dominance in arable fields) agrobiont spider in Hungary (SAMU & SZINETÁR 2002). However, this species is not an agrobiont in England and Western Continental Europe. It gains an agrobiont status along a NW-SE gradient in Central Europe (BLICK et al. 2000). The species has a second generation in Hungary (SAMU et al. 1998), while more northern populations are known to have a single generation (S. Toft pers. comm.). Although geographical details in the generation number shift have not yet been studied in detail, the fact that one generation populations are non-agrobionts or less dominant agrobionts (OBERG et al. 2008) suggests a relationship between generation number and the agrobiont status of the species. Since dominance increases from NW towards SE, and the existence of a second generation is known only from a starting point in Austria (ZULKA et al. 1997), we can infer the generation number to be an adaptation to climatic conditions. Since in Middle-Hungary the second generation was only facultative, i.e. part of the population had a one generation life-cycle, while the rest had two generations (KISS & SAMU 2005),

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submitted: 17.3.2010, accepted: 20.4.2010; online early: 10.1.2011

we suspected Hungary to be in a transition zone. Therefore we wanted to know if populations in NW Hungary and SE Hungary have different generation numbers.

We decided to conduct observations over a modest geographical gradient within Hungary. We wanted to study responses to climatic differences existing between the NW and SE parts of the country. The objectives were (a) agrobiont sub-assemblages (only the agrobiont species out of all spider species) – where we studied the species composition – and (b) the life history (generation number and timing of generations) of the most prominent agrobiont, *Pardosa agrestis* (Westring, 1861).

Material and Methods

Regional differences in agrobiont sub-assemblages

We studied the agrobiont sub-assemblages in 27 alfalfa and 21 cereal fields located in various regions of Hungary. Datasets with comparable sampling efforts and at least one cropping season sampling were selected from the Hungarian spider database (SAMU 2000). The sampling method was either suction sampling or pitfall trapping, or both in parallel (Tab. 1). Standard parametric and multivariate community analyses (MCCUNE & GRACE 2002) were run separately both by method and by the type of crop using PC-ORD, version 5.1.

Following SAMU & SZINETÁR (2002) we regarded a species as an agrobiont if its average dominance was higher than 1 % in arable fields and it occurred on at least 75 % of the fields. Thus the following species were arable agrobionts: *Pardosa agrestis* (Westring, 1861), *Meioneta rurestris* (C. L. Koch, 1836), *Oedothorax apicatus* (Blackwall, 1850), *Pachygnatha degeeri* Sundevall, 1830, *Erigone dentipalpis* (Wider, 1834), *Xysticus kochi* Thorell, 1872, and *Tibellus oblongus* (Walckenaer, 1802). The seven agrobiont species represented on average 75 % of the spider individuals in the studied fields (mean ± S.D. = 75.5 ± 16.05,

Table 1: Locations of fields considered in the study. Fields that belonged to the same settlement considered to have the same location. Fields by and large represent a NW-SW gradient, and pairings were made to maximise distance in this direction (see text for details).

				# of individuals (species) caught				
				alfalfa		cereal		*P. agrestis*
Settlement	Latitude (N)	Longitude (E)	# of fields sampled	pitfall	D-vac	pitfall	D-vac	study
Bánk	47° 53' 39"	19° 08' 50"	1				533 (18)	
Decs	46° 16' 41"	18° 46' 43"	2	155 (13)	277 (12)	317 (10)	203 (16)	80
Diósjenő	47° 55' 30"	19° 03' 01"	1		1961 (41)			
Felsőnána	46° 27' 46"	18° 32' 44"	6	4145 (61)	6348 (35)	576 (24)	660 (20)	2826
Fülöpszállás	46° 48' 39"	19° 11' 07"	3	210 (19)	2504 (42)	200 (17)	561 (26)	
Gencsapáti	47° 16' 54"	16° 35' 33"	1					586
Hatvan	47° 41' 17"	19° 36' 36"	1			3713 (96)		
Iclod	40° 59' 21"	23° 48' 52"	1	1741 (40)				
Kartal	47° 39' 20"	19° 32' 06"	2			2700 (77)		
Királyhegyes	46° 17' 03"	20° 41' 12"	3	763 (40)	244 (15)	161 (18)	111 (8)	538
Kunpeszér	47° 03' 33"	19° 17' 32"	4	55 (8)	81 (11)		118 (18)	
Kunszentmiklós	47° 00' 53"	19° 09' 17"	2		217 (10)		484 (16)	
Livada	47° 00' 18"	23° 50' 24"	1	1489 (33)				
Nagykovácsi	47° 32' 52"	18° 56' 03"	4	2867 (63)	8888 (76)	1176 (40)	1815 (39)	5556
Pásztó	47° 55' 12"	19° 44' 07"	1				146 (9)	
Páty	47° 32' 11"	18° 50' 49"	4		1259 (26)		313 (19)	
Rétság	47° 54' 34"	19° 05' 54"	1				333 (24)	
Romhány	47° 54' 36"	19° 12' 57"	1		1793 (41)			
Szekszárd	46° 19' 27"	18° 49' 23"	2	132 (10)		301 (16)	184 (13)	
Szombathely	47° 14' 58"	16° 38' 26"	2			4179 (37)		
Tevel	46° 22' 45"	18° 30' 28"	5	392 (27)	1474 (24)	152 (16)	96 (10)	319

N = 48 fields), while the remaining 25 % of the spiders belonged to 246 non-agrobiont species. The rare end of any community is always the most difficult to sample, and most vulnerable to undersampling bias. Therefore, when statistically considering the non-agrobiont species of spider assemblages (= non-agrobiont sub-assemblage), we only included those species into these analyses for which the whole data set had a cumulated individual count ≥ 50. Applying the inclusion rule, for the possible crop/method combinations we achieved the following number of non-agrobiont species: 29 spp. in alfalfa/pitfall; 28 spp. in alfalfa/D-vac; 32 spp. in cereal/pitfall and 25 spp. in cereal/D-vac.

We tested whether spider assemblages changed with geographical location by performing Mantel tests, with Monte Carlo simulation to derive significance (McCune & Mefford 2010). This tested for congruence between the geographical distance (Eucledian distance) of the study plots and the distance structure of the spider assemblages (Sørensen distance measure). Agrobionts and non-agrobionts were tested separately in the study plots.

We analysed data sets gained by the two sampling methods and in the two crops separately, and also treated the agrobiont and the non-agrobiont sub-assemblages separately.

Regional differences in *Pardosa agrestis* life history

We studied the generation numbers and the occurrence of first adult individuals in the common agrobiont wolf spider *Pardosa agrestis*. This comparison involved comparing fields along a NW – SE gradient during 6 sampling years (in the period 1993-2003) in pairwise comparisons, where in each year one northern and one southern population was compared, with a minimum distance of 126 km in between (see Tab. 1 for the sampling locations). Population samples were collected by pitfalls, emptied at weekly intervals.

Results

a) Regional differences in agrobiont sub-assemblages

The similarity structure of the analysed spider sub-assemblages was congruent with the geographic distance matrices, except for the alfalfa agrobiont sub-assemblage sampled by pitfalls. Relative to each other, the similarity between geographically close non-agrobiont sub-assemblages was always higher than it was between agrobiont sub-assemblages (Fig. 1).

Although average agrobiont similarity among fields was a moderate 37 % (Sørensen similarity, abundance data) it was nearly twice as high as the 20 % similarity among fields if non-agrobiont species were considered (a significant difference: paired t-test comparing average similarity – based on all possible field pairings – of the agrobiont and non-agrobiont sub-assemblages for each crop and sample method combination: t = 7.37, d.f. = 3, P = 0.005).

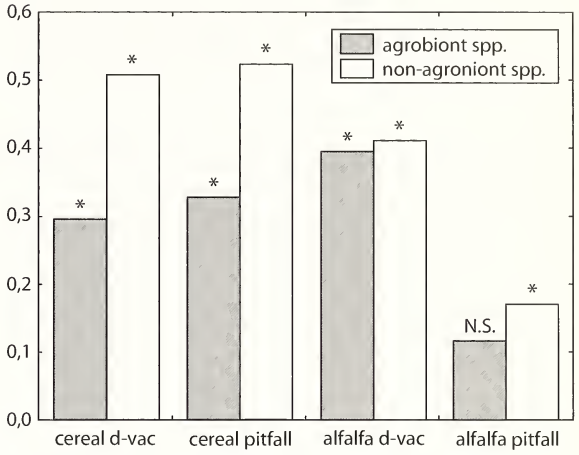

Figure 1: Standardised Mantel statistics of relationships between distances in the physical and in the community space separately analysed by (i) sub-assemblage type (agrobionts or non-agrobionts), (ii) crop type and (iii) collecting method. Asterisks denote the significance of the Mantel statistics at the P=0.05 level, obtained by Monte Carlo simulation.

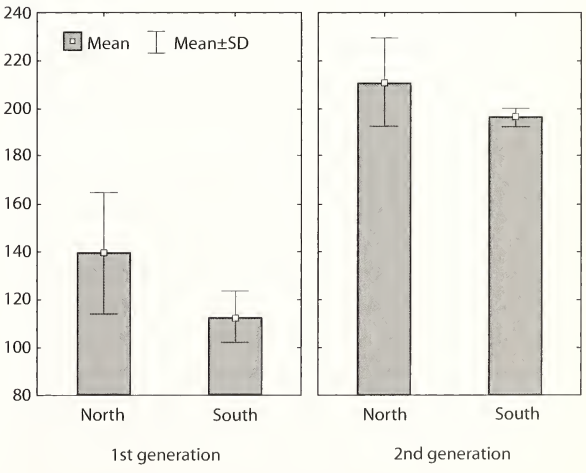

Figure 2: First occurrence of adult *P. agrestis* individuals in days counted from 1st January. Each year a new pair of northern and a southern populations (N = 6 pairs) were compared with a minimum distance of 126 km in between.

b) Regional differences in *Pardosa agrestis* life history

Comparing the northern and southern populations we found two generations in each year. Thus the basic pattern of *P. agrestis* life-cycle seems to be uniform across the country. The first adult occurrence of *P. agrestis* was significantly earlier in the more southern populations, on average by 16 days in the first, and by 14 days in the second generation (Fig. 2). The multi-factor ANOVA revealed that the effect of years was marginal, while interestingly, males did not occur significantly earlier than females in the samples (Tab. 2).

Table 2: ANOVA analysis result between first occurrences of adult *P. agrestis* individuals. The six studied years were taken as random factors. (* indicated by asterisk).

Source	SS	d.f.	F	P
Year*	1273.77	5	1.7706	0.1503
North-South	2466.78	1	17.1442	0.0003
Generation	60704.8	1	421.9015	0.0001
Sex	0.44	1	0.003	0.9565

Discussion

Agricultural habitats have very specific traits (such as special repeated pattern of disturbance (e.g. ploughing, harvest), monotypic, uniform vegetation structure, dominance of open soil surface, etc.), and the majority of the individuals – those belonging to agrobiont species – are adapted to these conditions (Wissinger 1997). Since crops have the same traits over large geographic areas, we expected the agrobionts to show little variation. Indeed, in the present study we found that similarity between agrobiont sub-assemblages was less determined by regionality (geographical proximity) than was the case for the non-agrobiont sub-assemblages.

Between-field similarity of agrobionts was much higher than that of non-agrobonts. We interpret these results to mean that while both agrobiont species composition and non-agrobiont species composition change geographically, the agrobiont composition is much more conservative and stable in this respect.

Moulting to the adult stage occurred ca. two weeks earlier in the southern populations of *P. agrestis* in the present study. Although the facultative nature of the two generations could not be studied by simple pitfall trapping, it can be speculated that more southern populations had more time to successfully complete a second generation and become juveniles that are large-enough for successful overwintering (Kiss & Samu 2002). Based on this finding, it can be hypothesised that *P. agrestis* populations in the south of Hungary are likely to have two obligate generations per year.

To summarise, the effect of regionality on agrobiont assemblages seems to be scalable down to relatively small geographical areas, such as Hungary. However, at smaller scales the effects become more subtle. Both in the structure of agrobiont spider assemblages and in the life history of a prominent agrobiont species, small but consistent regional differences could be observed within the country. Agrobiont assemblages were less affected than non-agrobiont species, which indicates that agroecosystems host fairly stable animal assemblages, and in those assemblages the agrobiont component is mostly affected by large-scale factors, such as climate. As opposed to agrobionts, some 25 % of the assemblages in the studied fields consisted of a high number of non-agrobiont species, which showed much stronger regional variability; presumably they were more influenced by neighbouring habitats. We believe that both the agrobiont and non-agrobiont components are important in the relationship between agricultural and natural areas, because natural areas can give shelter and increase the number of both types of species, while large and uniform arable land will homogenise and reduce regional species pools, which may negatively influence nearby natural habitats.

Acknowledgements

We are grateful for funding by the grant: OTKA T048434.

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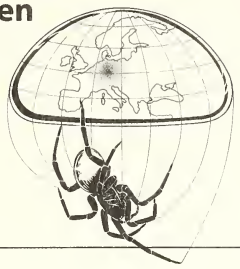

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ISSN 1018 - 4171 www.AraGes.de